QUANTIFYING SAURIAN TOOTH COMPLEXITY:

IMPLICATIONS FOR RECONSTRUCTING

THE DIET OF EXTINCT AMNIOTES

by

Keegan Michael Melstrom

A thesis submitted to the faculty of
The University of Utah
in partial fulfillment of the requirements for the degree of

Master of Science

in

Geology

Department of Geology and Geophysics

The University of Utah

May 2016

The University of Utah Graduate School

STATEMENT OF THESIS APPROVAL

The thesis of **Keegan Michael Melstrom**

has been approved by the following supervisory committee members:

Randall B. Irmis	, Chair	**3/8/2016** Date Approved
Allan A. Ekdale	, Member	**3/8/2016** Date Approved
Colleen G. Farmer	, Member	**3/8/2016** Date Approved

and by **John M. Bartley** , Chair/Dean of

the Department/College/School of **Geology and Geophysics**

and by David B. Kieda, Dean of The Graduate School.

ABSTRACT

Recent paleontological discoveries reveal a dramatic range of tooth morphologies in extinct reptiles, with some dentitions rivaling the complexity of extant mammals. Many of these dental morphologies have no modern analogs, inhibiting detailed dietary and ecological reconstructions for ancient ecosystems. Living saurian reptiles exhibit a wide range of diets, from carnivores to strict herbivores. Previous research suggests that the tooth shape in some lizard clades correlates with diet, but this has not been tested using quantitative methods. In order to elucidate the diet of extinct heterodont reptiles, I investigated the correlation between phenotypic tooth complexity and diet in living reptiles by examining the entire dentary tooth row in over 80 specimens comprising all major dentigerous saurian clades. I quantified dental complexity using orientation patch count rotated (OPCR), which does not require the identification of homologous landmarks on each tooth and discriminates diet in living and extinct mammals, where OPCR values increase with the proportion of dietary plant matter. OPCR was calculated from high-resolution CT scans, and I standardized OPCR values by the total number of teeth to account for differences in tooth count across taxa. In living saurians, OPCR values for omnivores and herbivores are higher than those of carnivores. In contrast with extant mammals, there appears to be greater overlap in tooth complexity values across dietary groups because multicusped teeth characterize herbivores, omnivores, and insectivores, and because the herbivorous skinks have particularly simple teeth.

Additionally, insectivorous lizards have dental complexities that overlap with omnivores. These results suggest reptilian tooth complexity is related to diet, similar to extinct and extant mammals. These data were used to reconstruct the diet of 14 extinct crocodyliforms. OPCR data indicate that extinct crocodyliforms occupied a larger ecological range than their living relatives. In particular, herbivory independently developed at least three times, with each occasion utilizing a different tooth morphology to break down plant material. These data, when combined with key morphological characters, allow for the dietary ecology of extinct organisms to be reconstructed.

TABLE OF CONTENTS

LIST OF FIGURES

Figures

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor, Randy Irmis. I could not have asked for a better mentor. He has guided me through every step of this process and has done so with the utmost support, wisdom, knowledge, and (most of all) patience. He has given me enough room to create my own research path and experience while also guiding me when I encounter unforeseen issues. Randy has helped shape my graduate school experience into something productive, successful, and fun; I do not know what I would have done without his help. I also want to thank Tony Ekdale and Colleen Farmer for serving on my committee and for their helpful feedback. I would like to thank the Department of Geology and Geophysics and the National Science Foundation Graduate Research Fellowship Program for their financial support.

Thanks to Lindsay Reader, William Sanders, and Joe Groenke for their help with the molding and casting process. Many thanks to Attila Ősi for his amazing casts of crocodyliform dentitions. I would like to thank Abby Vander Linden, Greg Wilson, Alistar Evans, and Doug Boyer for their help and guidance while I learned how to use the OPCR software. I could not have done this research without the help of an amazing group of curators and collections managers- Eric Rickart, Shannen Robson, Jessie Maisano, Patricia Holroyd, Jens Vindum, José Rosando, Matt Buehler, Jessa Watters, Laura Kabes, and Catherine Webb. I also want to thank Samer Merchant and Kent Sanders for their help μCT and CT scanning the casts, bones, and fossils.

I want to thank all of my friends for their help, support, and friendship, in

particular, Cornelia Rasmussen, Ellen Rosencrans, Dylana Watford, Jon Primm, Gabriela St. Pierre, Carl Beno, Daniel Hobbs, and Carla Valdes. I have gone on so many amazing adventures in the last two and a half years and I never would have had such wonderful experiences if not for them. I could not have imagined I would have met such an amazing group of people and formed the friendships we did in such a short amount of time. Lastly, I want to thank my family for all of their love and support. I could not have done all of this without them.

CHAPTER 1

INTRODUCTION

Amniotes, the group that includes living mammals and saurians, exhibit a wide range of dental morphologies. Many extinct amniote lineages have no closely related living representatives and/or possess tooth morphologies without modern analogs, making dietary reconstruction difficult. This research seeks to develop a methodology in which the diet of extinct amniote taxa with unusual dentitions can be confidently reconstructed. In particular, this research focuses on extinct crocodyliforms, which possess novel dental morphologies and postcranial adaptations, suggesting these animals were occupying ecological roles not seen in living crocodylians (Ősi, 2013). Such dietary inferences have direct bearing on reconstructing ancient ecosystem structures and how they changed through time.

Recent research has demonstrated a clear pattern between mammalian diet and tooth complexity, with carnivores possessing simple teeth, and herbivores having more complex dentitions (Evans et al., 2007; Santana et al., 2011), but this relationship remains unexplored in extant saurians. Unlike mammals, living saurians do not chew their food; instead, many swallow it whole or use repeated bites to slice and divide it before swallowing (Throckmorton, 1976; Schwenk, 2000). Regardless, dental morphology appears to play a key role in the breakdown of food because saurians display a wide disparity in dental morphologies.

For example, saurian carnivores often possess sharp, single-cusped teeth, whereas durophages, animals that preferentially consume hard-shelled invertebrates, possess labiolingually, mesiodistally expanded posterior teeth (i.e., wide, blunt teeth). Saurian omnivores, herbivores, and insectivores, a specialized category of carnivore, have a wide range in tooth morphologies. Some possess simple, peg-like morphologies (i.e., a cylindrical crown with a rounded apex), whereas others have labiolingually compressed (i.e., thin) multicusped dentitions.

In order to investigate the relationship between diet and dental complexity in living saurians, I examined 79 species from a wide variety of extant dentigerous saurian clades including crocodylians, squamates, and a rhynchocephalian. Dental complexity was quantified using a method called orientation patch count (OPC) in order to test for a potential relationship between diet and dental complexity. I then applied these data to a wide variety of extinct, heterodont crocodyliforms to reconstruct their diet based on the OPC values of their dentitions. Ultimately, this research seeks to use the diet of these extinct heterodont crocodyliforms to understand the ecological roles they played within their ecosystems and how these roles have changed through time.

Morphological Terms

Conical- A tooth with a wide, circular base and a single-cusped crown.

Dental complexity- The number of patches present on the occlusal surface of a tooth (i.e., the numerical representation of the three-dimensional tooth surface).

Dental morphology- The shape of a tooth.

Labiolingually compressed- The sides of the teeth facing the lips and tongue are expanded relative to the surfaces facing towards and away from the mandibular symphysis.

Occlusal- The surface of a tooth that interacts with the food an organism consumes.

References

Evans, A. R., G. P. Wilson, M. Fortelius, and J. Jernvall. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

Ősi A. 2013. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. Historical Biology 26:279–414.

Santana, S. E., S. Strait, and E. R. Dumont. 2011. The better to eat you with: functional correlates of tooth structure in bats. Functional Ecology 25:839–847.

Schwenk, K. 2000. Feeding in Lepidosaurs; pp. 175–291 in K. Schwenk (ed.), Feeding: form, function and evolution in tetrapod vertebrates.

Throckmorton, G. S. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agarnidae). Journal of Morphology 148:363–390.

CHAPTER 2

THE RELATIONSHIP BETWEEN DIET AND TOOTH COMPLEXITY IN LIVING SAURIAN REPTILES

Introduction

The clade Sauria comprises the two major branches of diapsid reptiles, Lepidosauromorpha and Archosauromorpha (Gauthier et al., 1988). Nonavian extant saurians are represented by over 10,000 species in two clades, Lepidosauria and Crocodylia (Uetz, 2015), which occupy a diverse range of ecological roles within their ecosystems (e.g., Reilly et al., 2007). These ecological differences, which include a variety of specialized diets (e.g., algae or pollen feeders) and lifestyles (e.g., burrowers, swimmers, gliders, or even taxa that can run across water), are particularly reflected in the wide morphological disparity among lepidosaurs (Snyder, 1949; Colbert, 1967; Nagy and Shoemaker, 1984; Cooper and Vitt, 2002).

Although most nonavian saurians are viewed as faunivores of some kind, more than half of studied species consume some plant material (Greene, 1982; Magnusson et al., 1987; Cooper and Vitt, 2002; Pauwels et al., 2007; Saalfeld et al., 2011; Laverty and Dobson, 2013). Approximately 12% of extant nonavian saurians are omnivores (i.e., animals that consume greater than 10% plants), with a minimum of 32 independent evolutionary origins of this dietary strategy (Cooper and Vitt, 2002). In contrast, herbivory is a comparatively rare development and is present in only 2% of extant

lepidosaurs and no extant crocodylians, although these numbers may increase with additional research because detailed dietary information is lacking for a large number of extant squamate species (Pough, 1973; Iverson, 1980; Jaksić and Schwenk, 1983; Zimmerman and Tracy, 1989; King, 1996; Cooper and Vitt, 2002; Espinoza et al., 2004). This paucity of herbivorous lepidosaur taxa has led to the suggestion that functional constraints restricting the development of herbivory exist in lepidosaurs (Sokol, 1967; Pough, 1973), although most of these studies ignore evidence for lepidosaur herbivory in the fossil record (King, 1996; Nydam, 1999; Nydam and Cifelli, 2005; Jones, 2009). The most widely cited hypothesis is that of Pough (1973), who posited that unspecialized lizards that weigh over 300 g must be herbivores due to metabolic requirements. Smaller animals generally have a higher mass-specific metabolic rate and require a greater caloric intake; therefore, lepidosaurs with a small body size are expected to be carnivores or insectivores. Recent studies have falsified this hypothesis, demonstrating that small (i.e., <300 g) lizards have evolved herbivory numerous times (Jaksić and Schwenk, 1983; Cooper and Vitt, 2002; Espinoza et al., 2004). For example, within just one group of South American iguanian lizards, Liolaemidae, herbivory has evolved separately approximately 18 times (Espinoza et al., 2004).

Tetrapod tooth morphology is generally thought to correspond to diet (e.g., Hotton, 1955; Presch, 1974; Evans et al., 2007), but there has been relatively little research conducted on the morphological specializations related to lepidosaur diet (but see Hotton, 1955; Throckmorton, 1976; Montanucci, 1989; Cooper and Vitt, 2002; Metzger and Herrel, 2005). Most existing research has focused on body size or specializations of the internal organs (Pough, 1973; Iverson, 1980; Troyer, 1984a, b;

Herrel et al., 2004; Herrel et al., 2008; Vervust et al., 2010). The few studies that have focused on dental shape suggest that tooth morphology correlates with diet in living lepidosaurs, but this idea has been tested infrequently and mostly qualitatively in scattered clades (Hotton, 1955; Montanucci, 1968; Robinson, 1976; Throckmorton, 1976; Sumida and Murphy, 1987; Mateo and López-Jurado, 1992; Barrett, 2000; Herrel et al., 2004; Vervust et al., 2010). In particular, it has been suggested that labiolingually compressed teeth with a varying amount of accessory cusps characterize herbivorous amniotes, largely based on comparisons with extant iguanid lizards (Hotton, 1955; Montanucci, 1968; Galton, 1986; King, 1996; Barrett, 2000; Reisz and Sues, 2000; Kley et al., 2010).

Across extant nonavian Sauria, dental morphology is quite disparate (Fig. 2.1; e.g., Edmund, 1969; Jones, 2009). Morphologies range from simple, peg-like teeth to enlarged posterior crushing teeth, to complex, multicusped heterodont dentitions (Fig. 2.1; e.g., Hotton, 1955; Presch, 1974; Dalrymple, 1979; Brizuela and Albino, 2009; Zahradnicek et al., 2014). Although a few authors have used qualitative methods to investigate the correlation between diet and tooth morphology, these studies have been limited in scope, focusing on single specific clades (e.g., teiids, lacertids, or iguanids) or a small number of phylogenetically distant heterodont lizards (Hotton, 1955; Presch, 1974; Estes and Williams, 1984; Mateo and López-Jurado, 1992; Herrel et al., 2004).

Several studies have used recently developed quantitative methods to assess tooth morphology in mammals. These studies demonstrate that phenotypic tooth complexity and diet are correlated in living carnivorans, rodents, bats, and primates (Evans et al., 2007; Bunn et al., 2011; Santana et al., 2011; Godfrey et al., 2012), as well as several

clades of extinct mammals (Boyer et al., 2010; Wilson et al., 2012; Evans and Janis, 2014). This method, called orientation patch count rotated (OPCR), allows for the direct quantitative comparison of dentitions between distantly related clades, including those that do not share easily identifiable homologous landmarks. In this contribution, I use OPCR to explore the correlation between tooth morphology and diet in living nonavian saurian reptiles. Specifically, I test the hypothesis that herbivorous reptiles possess more complex teeth than omnivorous or carnivorous taxa.

Methods

Specimens Studied

Extant Sauria includes a large diversity of edentulous taxa, most notably birds (Aves) and turtles (Testudines) (e.g., Crawford et al., 2012; Lyson et al., 2012; Field et al., 2014; Bever et al., 2015; Crawford et al., 2015). Because this study focuses on dental complexity, these clades are excluded from the dataset, and my usage of 'Sauria' focuses on dentigerous taxa within the clade (i.e., Lepidosauria and Crocodylia). I investigated the variations in dental complexity of extant reptiles and its relation to diet using a quantitative 3D geographic information system (GIS) analysis (Evans et al., 2007) applied to high-resolution surface models of complete lower jaw tooth rows. A total of 84 specimens from 64 genera and 79 species were studied (Table 2.1). Maximum taxon body size (snout-vent length) was either recorded from the specimen itself (before skeletonization) or taken from the literature. This sample spans a wide phylogenetic range from all major dentigerous saurian clades and includes one rhynchocephalian, six crocodylians, and 72 squamates (Fig. 2.2).

The specimens examined in this study span a broad range of dietary categories,

from hypercarnivores to strict herbivores. Dietary data, including percentage and types of organisms consumed, were obtained from peer-reviewed scientific literature. Because no quantitative definition of herbivory, omnivory, and carnivory exists, I follow the definitions of Cooper and Vitt (2002). Carnivores are defined as organisms that consume meat, primarily vertebrate material, for greater than 90% of their diet. Although the selection of 10% plant matter in a diet is arbitrary, it allows for animals that rarely or accidentally consume plant matter to still be considered carnivores. For instance, it is well documented that crocodylians consume some plant and fruit material, but this definition still classifies them as carnivores, a dietary assignment that is not in debate (McNease and Joanen, 1977; Delany and Abercrombie, 1986; Magnusson et al., 1987; Tucker et al., 1996; Pauwels et al., 2003; Pauwels et al., 2007; Saalfeld et al., 2011; Laverty and Dobson, 2013). Omnivorous diets include a percentage of vegetation varying between 10% and 90%, and therefore, herbivores are animals where plants make up over 90% of the diet (Cooper and Vitt, 2002). Similar to carnivores that consume small amounts of plant material, both mammalian and reptilian herbivores are known to occasionally, but purposely, consume animal material (e.g., Loftin and Tyson, 1965; Iverson, 1979; Greene, 1982; Furness, 1988a; b).

Two additional dietary categories that are special cases of carnivory are included in this analysis: durophages and insectivores. Durophages are defined as animals that preferentially consume hard-shelled organisms, such as snails or mollusks. Although their diet can include a variety of plant, invertebrate, and vertebrate material, in this dietary category hard-shelled prey make up a large portion of their diet. Unfortunately, volumetric dietary data are lacking for the studied durophages, making the exact

percentage of hard-shelled organisms in their diet unknown. Insectivores, similar to other carnivores, are defined as organisms whose diet is over 90% animal material, although they are distinguished from carnivores by their reliance on arthropod prey (e.g., insects), rather than vertebrate prey. This distinction between categories was made because previous work indicated insectivores potentially have separate factors influencing their tooth complexity (Strait, 1993; Evans et al., 2007; Santana et al., 2011).

To the best of my knowledge, all specimens studied were adult individuals, because previous studies have documented that a number of lizard taxa undergo an ontogenetic shift in diet, from insectivores to herbivores (Montanucci, 1968; Nagy and Shoemaker, 1984; Duffield and Bull, 1998; Rocha, 1998; Durtsche, 2000; Cooper and Vitt, 2002). This dietary shift and its potential correlation with tooth morphology (i.e., ontogenetic changes in dental complexity) were not investigated.

I sampled the complete tooth row of the left dentary in extant lepidosaurs and crocodylians (Fig. 2.3A), although the right dentary and upper tooth row (premaxilla and maxilla) were also measured in a small subset of specimens in order to compare the dental complexities within the same specimen (Table 2.1). No palatal teeth were included in the complexity analysis. Unlike previous mammalian OPCR studies that measured only the molars (Santana et al., 2011) or premolars and molars (Evans et al., 2007; Boyer et al., 2010; Wilson et al., 2012), I investigated the complexity of the complete tooth row, because most saurian taxa lack a discrete change between simple anterior teeth (incisiform) and complex posterior teeth. Unlike in mammals, which have discrete regions of the dentition, this lack of regionalization makes it difficult and highly subjective to identify where to start the analysis. Therefore, in order to reduce any

potential bias the entire tooth row was measured.

The sampled saurians have a worldwide geographic range, with multiple specimens coming from every continent except Europe and Antarctica. Nearly half of the sampled taxa were from the iguanid clade, whereas scincoids, lacertids, and anguimorphs are also well represented, with nine, 13, and eight taxa included, respectively. In five cases, two specimens of the same species were examined to address potential individual variation. Sampled taxa span a range of tooth morphologies, in order to quantify the individual variation that exists between lizards with simple and complex teeth. Multiple species from the same genus were also measured to examine intra-genera differences. This includes two species from *Brachylophus*, *Chamaeleo*, *Crotaphytus*, *Ctenosaura*, *Cyclura*, *Egernia*, *Gerrhosaurus*, *Leiocephalus*, *Sceloporus*, and *Tupinambis* each, three species of *Basiliscus*, and five species of *Varanus*.

Data for the study were collected from nine museum collections, and 33 CT scans were obtained from Digimorph CT repository at University of Texas at Austin. Most of the Digimorph scans were originally included in Gauthier et al. (2012) for their study of squamate phylogeny. Specific details on the resolution and additional information of each scan are available on Digimorph. Specimens from the Sam Noble Museum of Natural History at the University of Oklahoma, the Museum of Comparative Zoology at Harvard University, the University of Kansas, the National Museum of Natural History (the Smithsonian Institution), and the San Diego Natural History Museum were obtained on loan and μCT scanned at the University of Utah Small Animal Imaging Core Facility. Specimens that could not be directly μCT scanned were molded (see below) at their respective institution and the casts were μCT scanned at the University of Utah Small

Animal Imaging Core Facility.

Molding and Casting Procedure

Thirty-nine specimens were molded at the California Academy of Sciences, the Museum of Vertebrate Zoology at Berkeley, and the University of California Museum of Paleontology. The molds and casts are reposited in the paleontology collections of the Natural History Museum of Utah. These molds were made using Reprosil light body catalyst and base molding material. Casts were made using EPOTEK 301 epoxy resin, which has a submicron resolution (Teaford and Oyen, 1989). Specific details of the molding and casting procedure are reported in the Appendix.

CT Scanning and 3D Model Editing

Casts and loaned skeletal items were scanned at the University of Utah Small Animal Imaging Core Facility. A Siemens INVEON μCT scanner digitized each jaw at a voxel resolution of 35 microns, a voltage of 80 kVp, and a current of 150 μA. Multiple specimens were often scanned together (up to nine at once) at a pixel resolution of 1152; each scan comprised 1,984 to 2,016 slices. Dr. Kent Sanders (Department of Radiology, University of Utah Hospital) scanned two additional specimens, *Paleosuchus trigonatus* and *Varanus olivaceous*, that could not fit into the μCT scanner at the University of Utah Medical Center on a Siemens single source medical CT scanner. *V. olivaceous* was scanned at a pixel resolution of 512 for 276 slices and *P. trigonatus* for 500 slices, each at a slice thickness of 0.4 mm. Both were scanned at a voltage of 120 kVp, but the current varied, 360 μA for *V. olivaceous* and 37 μA for *P. trigonatus*. CT and μCT data were exported from the native scanning software in DICOM format. These image stacks were

imported, cropped, and converted into TIFF stacks using ImageJ (National Institutes of Health, Bethesda, MD, USA). TIFFs were then converted into STL 3D surface model files and opened in MeshLab 1.3.3 (http://meshlab.sourceforge.net/). Extraneous cast material and unnecessary skeletal elements were digitally removed from the 3D reconstructions in MeshLab, isolating the dorsal-most portion of the left dentary and teeth (Fig. 2.3B). Scans were oriented with the occlusal surface parallel to the z-axis in the 3D analysis software Avizo (version 7.0.1) and subsequently exported into an STL (ASCII) file.

OPCR Analysis

The digitized dentition was converted from STL to a Surfer grid file using Surfer 8 for Windows (Golden Software Inc.). The software package Surfer Manipulator was used to compute complexity for the entire tooth row (Evans et al., 2007). The surface complexity of the tooth row is quantified using a technique that does not require the use of homologous landmarks called orientation patch count (OPC). OPC is calculated by determining the orientation of each pixel in the 3D scan and grouping contiguous pixels with a similar orientation (based on their cardinal and ordinal directions). Each group of two or more adjacent pixels with a similar orientation is called a patch (Fig. 2.3D). The more patches a tooth row has, the more complex the dentition. Because OPC takes into account orientation and not height, tooth replacement stage is removed as a factor that may otherwise affect complexity measurements.

Surfer Manipulator (in the *File Format Conversion* window) converts the edited 3D reconstructions into topographic maps (Fig. 2.3C). The STL file is loaded into Surfer Manipulator and is exported as a .grd file. The default grid interval is .03 mm (30

microns), and increasing this value to 1–4 mm (although this value can be significantly higher) allows for the dentition in this study to be analyzed without scan artifacts to appear, such as pitting (i.e., small divots appearing in the topographic map). Grid intervals below 1 mm typically cause Surfer Manipulator to crash.

Once the .grd files have been generated, the dentition must be isolated from the dentary and scaled (in the *Surfer Functions* window). The dentition is cropped by outlining the occlusal surface of each tooth in Surfer. Portions of the tooth that do not interact with food (i.e., are below the gum line) are also excluded during this step. The .grd file is then 'blanked' (i.e., cropped), which leaves only the teeth available for complexity analysis. During this step, choosing to 'regrid' the digitized dentitions will affect the size (i.e., resolution) of the teeth at which complexity is interpreted.

Previous studies on mammalian dentitions scaled all tooth rows to the length of 150 data rows, thereby removing the effect of size on complexity (Evans et al., 2007; Santana et al., 2011; Wilson et al., 2012). Because the number of molars and premolars in eutherian mammal jaws has minimal variation (between 1–4 teeth in Evans et al., 2007) compared to reptiles, this standardization corrects for absolute size. Such a scaling method cannot reliably be applied to reptilian dentition, as living reptiles display a remarkable variability in tooth count between species (Edmund, 1969). Taxa in this study possessed dentary tooth counts that vary from five to 33 teeth; therefore, the number of data rows was standardized by the number of teeth. This study investigated the dental complexities at three levels of resolution: 25, 40, and 50 data rows per tooth (RPT; Fig. 2.4). Therefore, this study holds the size of the tooth constant, as opposed to the size of the tooth row (Boyer et al., 2010; Smits and Evans, 2012; Evans and Janis, 2014). In

many cases, the number of mammal teeth in a tooth row is three, which allows for the direct comparison of saurian and mammalian complexity values at the level of 50 RPT.

Although 50 RPT allows for the greatest volume of detail to be analyzed and direct comparison with previous studies of mammals, it also has a number of drawbacks. Minute imperfections in jaw casts are often detected and quantified, causing an artificial increase in complexity. At this resolution (50 RPT) there is also a disparity between μCT scans and Digimorph scans, with the latter having lower complexity values (Fig. S.2.1). This disparity likely reflects the limit of resolution for the Digimorph scans, though lower resolution scans can also have higher complexities due to pixelated surface textures (i.e., individual polygons of surface scans are counted as patches). Lastly, complex dentitions or dentaries with a large number of teeth can cause Surfer Manipulator to crash at 40 and 50 RPT, restricting the maximum number of patches that can be recorded. Although 25 RPT captures less detail, these issues are mitigated for my dataset, and these results were used for most of this study (for an in depth discussion of the number of data rows to use, see Evans and Janis, 2014).

Using the blanked files, Surfer Manipulator can analyze dental complexity (in the *CSV Viewer* window). Each tooth is broken into discrete patches based on surface orientation. The topographic maps generated earlier are used to determine the orientation at each grid point based on one of the eight compass directions (e.g., North, Northwest, West), and these grid points are then grouped together to create patches. The number of patches (two or more adjacent pixels) is then computed, which generates a numerical representation of dental complexity (Fig. 2.3D). In order to mitigate the effect of minor variations in orientation between scans, the OPC calculation is repeated eight times at

intervals of 5.625°, with the mean value of these repetitions being used to generate complexity values: orientation patch count rotated (OPCR; Smits and Evans, 2012; Wilson et al., 2012; Evans, 2013).

I employed three different methods for evaluating OPCR data. The first looked at the total OPCR of the jaw (i.e., raw OPCR values; OPCRt). The second method divided the total OPCR value of the jaw by the number of teeth measured, calculating the average OPCR per tooth (OPCRavg). Finally, I analyzed the OPCR values (at 25, 40, and 50 RPT) of the most complex individual tooth for each specimen (OPCRit). This tooth was often from the distal portion of the dentary (Table S.2.4).

Statistical Analyses

I tested whether differences in OPCR values between all dietary categories were statistically significant using a Kruskal–Wallis test. Pairwise differences between individual dietary categories (e.g., omnivore vs. insectivore) were evaluated with Mann–Whitney *U*-tests. Both tests were conducted using the PAST software package (Hammer et al., 2001).

I also conducted several phylogenetically-informed comparative tests with these data. Hypothesized squamate phylogenetic relationships vary widely between studies, with major conflicts existing between molecular and morphological analyses. Among the three phylogenetic typologies I used for these comparative tests, Gauthier et al. (2012) used morphological character data, Pyron et al. (2013) used a large molecular dataset, and Reeder et al. (2015) conducted a combined analysis of morphological and molecular data, with the addition of several fossil taxa. To compute branch lengths for these phylogenies, divergence data were sourced from Hedges et al. (2015).

Using these phylogenies, I conducted a phylogenetically independent contrasts (pIC) analysis to investigate whether phylogeny has an influence on the correlation between tooth complexity and diet. pIC is a comparative method that assesses whether two continuous traits, average tooth complexity (OPCRavg) and percentage of plant matter in diet in this study, have evolved in conjunction (Baum and Smith, 2013). This test uses Brownian motion to reconstruct the value of both traits at each ancestral node, which are then compared with each other. By reconstructing the ancestral states and then comparing these values to each other, this helps correct for potential correlation resulting from phylogeny alone. The pIC tests were conducted using the PDAP module (version 1.16) for the Mesquite software package (version 3.03; Midford et al., 2005; Maddison and Maddison, 2006). The pIC comparisons were limited to taxa where a quantitative estimate of plant material in the diet was available (Table 2.1). Volumetric data were chosen because they are more common and reliable than other metrics, such as fecal data, of reporting dietary information (see Cooper and Vitt, 2002). Therefore, only 71 taxa were included in the pIC analysis.

Results

Extant saurians exhibit substantial variation in dental morphology and complexity, similar to living and extinct mammals (Figs. 2.5–13; Evans et al., 2007; Boyer et al., 2010; Santana et al., 2011; Godfrey et al., 2012; Wilson et al., 2012). Reptiles with different diets were found to have different complexities, with a general increase in complexity values from carnivores to herbivores– carnivores having simpler teeth, on average, than omnivores or herbivores.

Tooth Complexity

Carnivores

Thirteen carnivores were included in this study and include six crocodylians, three varanids, one snake, one amphisbaenian, and two additional lizards, *Crotaphytus bicinctores* and *Heloderma suspectum*. Although there was significant variation observed for the total and average tooth complexity values (OPCRt and OPCRavg, respectively), this group had the simplest teeth of all measured dietary categories (Fig. 2.5). Variation in dental complexity values reflects the broad range in carnivorous tooth morphologies (Fig. 2.6). For example, the snake *Coluber constrictor* possesses 11 recurved teeth with high tip sharpness (i.e., radius of curvature at the cusp tip; Evans and Sanson, 1998), whereas the crocodylian *Alligator mississippiensis* has 17 teeth that range from a conical, blunted morphology, to more bulbous-shaped teeth in the posterior dentary. When evaluating the OPCRavg, the simplest teeth are present in animals from disparate phylogenetic positions: the crocodylian *Gavialis gangeticus* (1.30 patches per tooth [PPT] at 25 RPT) and the anguimorph *Heloderma suspectum* (1.325 PPT). These values change little as the RPT of the scan is increased (Table S.2.3).

Using 25 RPT, the majority of carnivores have an OPCRavg between 6 and 8 (Fig. 2.5). The carnivore with the highest tooth complexity is *Crotaphytus bicinctores* (8.65 PPT) and is characterized by 22 small, conical, sharp teeth (Fig. 2.6A). This slightly higher average tooth complexity results from the round tooth profile in occlusal view. Teeth with fewer than 8 PPT are labiolingually compressed, and, therefore, fewer cardinal directions are represented (e.g., the knife-like, thin teeth of *Varanus varius*).

Total dentary OPCR shows a similar pattern in complexity to OPCRavg (Fig.

2.5A). Carnivore values vary between 9.75 (*V. varius*) and 190.375 (*C. bicinctores*) patches. The disparity between total OPCR values is mainly a result of the number of teeth in the dentary. Carnivores have a wide range in tooth number within the dentary, from 5 (*H. suspectum*) to 22 (*C. bicinctores*). Similar to the OPCRavg, the OPCRt increases in 40 and 50 RPT trials, but the overall pattern does not change (Table S.2.2). OPCRit shows a similar pattern to the other tests (Fig. 2.5C; Table S.2.4), the only major difference being that *Varanus rudicollis* possesses the simplest tooth (6.25 patches; Fig. 2.4).

There is no significant relationship between either OPCRt and body size or OPCRavg and body size (Fig. 2.7). The carnivores in this sample span a wide range in body sizes from approximately 110 mm (maximum snout-vent [SV] length) in *C. bicinctores* to over a meter in *V. salvator* and several meters in the crocodylians. The smallest carnivore has the greatest OPCRavg value, whereas the largest carnivores (crocodylians) have a large disparity in OPCRavg values (1.31–7.19 PPT). This result strongly suggests that body size has little effect on dental morphology and complexity.

Durophages

Durophagous animals are a special category of carnivores that preferentially consume hard-shelled organisms. The two molluscivores in this study, the squamates *Varanus niloticus* and *Dracaena guianensis*, are characterized by mesiodistally and labiolingually expanded posterior teeth (Lönnberg, 1903; Edmund, 1969; Presch, 1974; Dalrymple, 1979; Rieppel and Labhardt, 1979; Estes and Williams, 1984; Losos and Greene, 1988) and, although they both consume hard-shelled organisms, their complexity values differ (Fig. 2.8). *V. niloticus* possesses relatively simple teeth, with an OPCRavg

of 5.65 PPT and an OPCRt of 45.25 at 25 RPT. In contrast, *D. guianensis* possesses more mesiodistally and labiolingually expanded teeth relative to *V. niloticus* and has an OPCRavg of 8.93 PPT and an OPCRt of 80.375. *D. guianensis* on average has more complicated teeth than any other carnivore, although the OPCRt value is lower than many other carnivores, because this specimen only possesses nine teeth in the left dentary (Fig. 2.5).

At 40 and 50 RPT, the average tooth complexity of both species increases, *D. guianensis* more so than *V. niloticus*. At 50 RPT *D. guianensis* possesses the most complicated average tooth (OPCRavg) of any nonherbivorous lepidosaur. The OPCRt does fall in the middle of carnivore complexities in both 40 and 50 RPT trials and is below most insectivore, omnivore, and herbivore values (Fig. 2.5A).

Individual durophagous teeth are equal to or more complicated than other carnivorous animals at 25 RPT; both *D. guianensis* and *V. niloticus* have higher complexity values than all carnivores except *C. bicinctores* (9 PPT; Fig. 2.5C). When the RPT is increased, values for *D. guianensis* teeth remain higher than all other carnivores, whereas *V. niloticus* has lower complexity values than *V. rudicollis* and *H. suspectum* (Table S.2.4).

Insectivores

Although the 24 insectivores measured possess a wide range of dental morphologies (Fig. 2.9), they have the narrowest range of OPCRavg values at 25 RPT (aside from molluscivores, which is probably a sample size issue given there are only two taxa) (Fig. 2.5). These values fall between 6.26 PPT (*Chamaeleo senegalensis*) and 11.125 PPT (*Basiliscus vittatus*). At 25 RPT, OPCRt values vary between 49.625 (*Bipes*

canaliculatus) and 264.5 patches (*Hemitheconyx caudicinctus*; Fig. 2.5). These values are generally higher than carnivorous taxa and slightly lower than, but largely overlapping with, omnivorous taxa. When the OPCRt is measured at increased resolutions, this pattern changes. At 40 RPT, insectivores possess more complex teeth than many omnivores, with only one omnivore possessing a more complex dentition than insectivores (*Basiliscus plumifrons*). In both high-resolution analyses the simplest dentitions of insectivores were more complex than the simplest dentitions of carnivores, molluscivores, and omnivores. The key result is that, no matter the RPT used in the analysis, there is significant overlap in tooth complexity values for insectivores and omnivores.

The isolated teeth of insectivores display a greater range of complexity values than other dietary categories besides herbivores (Fig. 2.5C). Isolated tooth complexities range from the relatively simple teeth of *Hemitheconyx caudicinctus* (6.75 PPT) to the multicusped teeth of *Kentropyx pelviceps* and *Calotes mystaceus* (14.125 and 14.5 PPT, respectively; Fig. 2.5C). At 25 RPT, the dental complexity value range is greater than the entire range of omnivores. At higher RPTs the tooth complexity ranges of omnivores and insectivores are nearly identical.

Specimens that were investigated for this study occupy a narrow range in body sizes, between 60 and 300 mm SV length, whereas there is a large disparity in OPCR values (Fig. 2.7). Smaller taxa (<150 mm) possess both complex (10.9 PPT for *Plica* umbra) and simple (7.02 PPT for *Elgaria coerulea*) OPCRavg values at 25 RPT. Only one insectivorous taxon was sampled with a maximum SV length greater than 200 mm, *Chamaeleo senegalensis*, which possesses relatively simple teeth (6.26 PPT at 25 RPT).

Therefore, similar to carnivores, there is a very weak, if any, relationship between body size and OPCRt and OPCRavg values in insectivorous saurians.

Omnivores

The dental complexity of the 26 sampled omnivore species significantly overlaps with that of insectivores and herbivores (Fig. 2.5). The OPCRavg values range from *Platysaurus guttatus* (6.4 PPT) to *Basiliscus plumifrons* (12.015 PPT). Significant morphological variation exists among omnivorous lepidosaur dentitions, for example; blunted (i.e., low tip sharpness) tricuspid teeth, with a tall central cusp bordered by mesial and distal lower cusps characterize the dentition of *B. plumifrons*, whereas *P. guttatus* possesses simple conical teeth unadorned by additional cusps (Fig. 2.10). Higher resolution analyses at 40 and 50 RPT result in OPCRavg values (between 7.5–15 and 8.4–17.5 PPT, respectively) that are nearly identical to those observed in insectivores.

Similarly, OPCRt values of omnivorous saurians nearly completely overlap with insectivores at 25 RPT, ranging from 59.625 (*Varanus olivaceus*) to 300.375 (*B. plumifrons*) patches (Fig. 2.5B). This overlap in complexities is also observed in the analyses at 40 and 50 RPT analyses, although there are four omnivores with lower complexities than any observed in insectivores (a result of having fewer teeth).

At 25 RPT omnivores have a lower range of isolated tooth complexities than insectivores (Fig. 2.5C). The bicuspid posterior teeth of *Teius teyou* have the highest complexity (13.75 PPT), but at 50 RPTs the tricuspid *Cyclura pinguis* has the most complex teeth (23.75 PPT). At all resolutions the tooth complexities of sampled omnivores and insectivores are nearly identical.

Omnivores in this study have a wide range of maximum SV lengths, from 70–730

mm, with a greater proportion of larger (>200 mm) animals than insectivores. Similar to insectivores, saurians smaller than 200 mm have a large disparity of complexity values (6.4–11.73 PPT at 25 RPT). This contrasts with taxa above 250 mm, which have no measured OPCRavg values above 9 PPT. Although the R^2 value is low, the general trend illustrates a slight decrease in dental complexities in larger saurians. This result contrasts with previous dietary groups, in which no clear trend is discernable.

Herbivores

Herbivores have the largest range in dental complexity values of any dietary category, ranging from an average tooth complexity (at 25 RPT) of 5.69 PPT in *Cyclura carinata* (although this is likely artificially low - see Discussion) to 18.03 PPT in *Amblyrhynchus cristatus* (Fig. 2.5). Multiple cusps or serrations typically characterize these high-complexity dentitions (Fig. 2.11). With higher RPTs, the pattern for OPCRavg is more pronounced, with dental complexities reaching values as high as 31.9 PPT (*A. cristatus*) at 50 RPT (Table S.2.3). Not all herbivores display complex dentitions. Skinks, such as *Tiliqua rugosa* and *Egernia stokesii*, possess simple, conical or labiolingually compressed teeth (Fig. 2.11A). Additionally, even some iguanids with what appear to be complex dentitions have low complexity values at 25 RPT. In these cases, the taxa in question often have minute cusps or serrations, which are too small to be resolved separately by the OPCR analysis at 25 RPT (see discussion); examples include *Iguana iguana* and *Cyclura carinata*.

Similar to the OPCRavg values, OPCRit values of herbivores have the greatest range, from 7.75 (*Ctenosaura pectinata*) to 18.75 PPT (*Amblyrhynchus cristatus*) at 25 RPT (Fig. 2.5). At 40 and 50 RPT, many teeth that have otherwise low complexities at 25

RPT substantially increase in complexity (e.g., *Brachylophus vitiensis*, *Cyclura carinata*; Table S.2.4). This increase is largely a result of better detection of small cusps and serrations. The OPCRt is generally higher for herbivores than other dietary categories (Fig. 2.5A). The minimum observed herbivore OPCRt value is greater than the minimum observed omnivore OPCRt value at all resolutions.

Herbivores also display a reduced range in body sizes, with the largest taxa no greater than approximately 400 mm maximum SV length. This range in body sizes has been noted by more recent studies of herbivorous lizards (Espinoza et al., 2004), and clearly demonstrates that herbivorous lizards are not restricted to sizes greater than 300 g (contra Pough, 1973). Similar to previous dietary categories the OPCRt and OPCRavg values decrease at larger body sizes, although the greatest disparity in complexities occurs at a slighter larger body size than previous groups (Fig. 2.7). This relationship between dental complexity and body sizes is tentative, but it appears as though larger (>300 mm) noncarnivorous saurians generally have lower dental complexity values.

Discussion

This research demonstrates that tooth complexity correlates with diet in living lepidosaurs and crocodylians. Although there is more overlap in tooth complexity values between dietary categories than in extant rodents and carnivorans, it indicates that diet is an important factor in determining dental morphology even in animals that do not possess precise occlusion or extensively orally process food. This result suggests these data can be used as a modern baseline to help reconstruct the diet of extinct dentigerous amniotes, even those without close living relatives or clear modern analogs.

Caveats in Interpreting Results

Variation in OPCR Results

To ensure the reliability and repeatability of these data, I conducted a number of tests to address the variation in OPCR values. To test for the effect of different tooth orientations, I rotated oriented jaws by approximately three degrees in the x-plane. This test ensured that slight subjective variations in orientation would not dramatically affect the overall result of each OPCR test. Additionally, I edited and reoriented tooth rows a second time to test the repeatability of each orientation. In both cases (16 repeated taxa in 21 trials) there was typically less than one patch per tooth difference, indicating no significant change in the OPCR values.

For three taxa, I investigated how much variation exists between specimens of the same species. Individual variation was found to be minimal in the measured specimens. In different specimens of *Gerrhosaurus major*, *Iguana iguana*, and *Uromastyx aegyptia*, differences between average OPCR per tooth were less than 1 patch per tooth (PPT) at 25 rows per tooth (RPT). When these dentitions were analyzed at 40 and 50 RPT there was less than a 2 PPT difference. OPCRt differences were higher, as different specimens possessed different numbers of erupted total teeth per jaw.

In only one OPCRavg test, *Basiliscus basiliscus*, was there a complexity difference of greater than 1 PPT at 25 RPT, and this difference is likely due to the differing quality of scans (μCT vs. CT) combined with the dramatic difference in tooth number (11 tooth difference). Even with the much higher resolution of the μCT scan recording significantly more phenotypic information, the difference between the Digimorph and μCT scanned specimen is less than 2 PPT.

When evaluating differences between species in the same genus there was significantly more variation. For example, there is a nearly 4 PPT difference at 25 RPT in the genus *Basiliscus* (3.9 PPT) and a 6 PPT difference in *Varanus* (5.9 PPT). This variation makes sense given that individual species within these genera vary with respect to their diet, giving confidence that the OPCR analysis can detect a phenotypic difference in tooth complexity in closely related species. In other genera there was very little difference in dental complexity; for example, *Crotaphytus bicinctores* and *C. collaris* are separated by slightly more than 1 PPT difference, whereas the differences between *Egernia striolata* and *E. stokesii* was less than 1 PPT. In the case of *Egernia*, the species that consumes a greater volume of plants possesses a slightly higher tooth complexity value.

These results suggest that even with differences in scan quality, tooth orientation, and tooth count, the OPCR analysis is robust enough to reflect actual variations in tooth complexity rather than data noise. Differences and similarities in complexity values between species, therefore, reflect the observed morphology, not artifacts of analysis.

Scan Quality and Analysis Resolution

The dental complexity of 33 lepidosaur and crocodylian specimens was measured from CT scans which were conducted between the late 1990s and mid 2000s by the University of Texas at Austin High-Resolution CT lab, and are available on Digimorph. In contrast, μCT scans were conducted more recently at the University of Utah Small Animal Imaging Core Facility. These μCT scans are much higher resolution than those from Digimorph. Therefore, this disparity in scan resolution affects observed OPCR values. To address this issue, I separated the specimens into three categories, CT scans

obtained from Digimorph, μCT scans of casts, and μCT scans of original specimens, and assessed whether there were systematic differences in OPCR values.

When evaluating both the OPCRavg and OPCRt there was significant overlap between all three categories at 25 RPT. When the scan resolution was increased to 40 and 50 RPT a clear difference in values was apparent, with μCT scans of casts yielding generally greater OPCR values than the Digimorph scans, although there was minor overlap (Fig. S.2.1). For this reason, I prefer 25 RPT to analyze scan data with OPCR and interpret the results in this study, because it captures enough complexity information to distinguish major features (e.g., cusps), but does not produce systematic bias between results from the μCT and Digimorph CT scans.

One limitation of the OPCR analysis at 25 RPT is that it can ignore fine details present on the dentition, which artificially lowers complexity for some taxa. This issue is most pronounced in two herbivorous squamate taxa, the iguanids *Iguana iguana* and *Cyclura carinata*. *I. iguana* possesses compressed, leaf-shaped teeth with 15–20 extremely fine cusps/serrations on the margins (Throckmorton, 1976). These serrations are not detected at 25 RPT, and, therefore, their complexity is not reflected in this OPCR result, but these cusps are detected at 40 and 50 RPT. *C. carinata* is the most extreme example of this artificial lowering of complexity at 25 RPT. Similar to *I. iguana*, the majority of dentary teeth are labiolingually compressed and possess 3–4 cusps on each mesial and distal margin, cusps that are more prominent than those observed on *I. iguana*. These cusps are not detected by the 25 RPT OPCR analysis, leading to the OPCRavg value of 5.69 PPT, a value lower than any insectivore or omnivore. Therefore, care should be taken when interpreting OPCR at lower resolutions (<40 data rows per tooth),

especially when these teeth are labiolingually compressed with a fine cuspate morphology.

Labiolingually compressed teeth with varying degrees of small cusps are common in iguanid herbivores (Fig. 2.11D, 2.14; Barrett, 2000), which suggests that the complexity values of these particular herbivorous taxa are likely underestimated. Even with the conservative complexity estimation, herbivores have higher average complexity values than other dietary groups ($P < 0.0001$ for Kruskal–Wallis test).

Heterodonty

Another factor that lowers complexity estimations of noncarnivore saurian taxa is the presence of simple conical shaped teeth in the mesial portion of the dentary. These teeth are rarely described or figured in studies of herbivorous lepidosaur dental morphology, although they have a distinct morphology when compared to more distally positioned teeth (Barrett, 2000). In a number of taxa, including iguanids, the mesial dentary teeth are recurved, nearly circular in cross-section, and terminate in a single, sharp point, in contrast to the more posterior multicusped teeth (Figs. 2.9–12; Hotton, 1955; Barrett, 2000). These mesially-positioned teeth are nearly identical to carnivorous taxa. However, most carnivorous taxa are relatively homodont (Figs. 2.6, 2.12); therefore, their simple morphology has no net effect on the OPCRavg. In contrast, in these heterodont taxa the anterior teeth are significantly simpler than the posterior dentition, lowering the OPCRavg (Fig. 2.12). This effect lowers the OPCRavg of durophages, insectivores, omnivores, and herbivores and likely contributes to more overlap in OPCR values between dietary categories than in mammals. The exclusion of these simpler mesially placed teeth in all taxa (as has been done in mammalian studies by

restricting analysis to postcanine teeth) might provide more separation in OPCR values, but this elimination would be subjective given that extant saurian dentitions lack the discrete regionalization observed in mammals.

Diet and Tooth Complexity in Extant Saurians

Among dentigerous saurians, there is a clear gradation in dental complexity from simple teeth in carnivorous taxa to more complicated teeth in herbivores ($P < 0.0001$ for Kruskal–Wallis test; Fig. 2.5). This relationship is present in all three measures of dental complexity at 25 and 40 RPT, OPCRt, OPCRavg, and OPCRit. At 50 RPT this pattern is not as clear, with insectivores possessing more complex teeth than omnivores, although this may be an artifact of the low-resolution Digimorph scans. A number of previous studies have suggested that diet correlates with tooth morphology in extant lizards, but these have investigated only isolated lizard clades using qualitative methods (e.g., Hotton, 1955; Mateo and Montanucci, 1968; Presch, 1974; Estes and Williams, 1984; Sumida and Murphy, 1987; López-Jurado, 1992; Barrett, 2000; Herrel et al., 2004; Vervust et al., 2010). This is the first study to apply quantitative methods to assess the correlation between tooth complexity and diet in all living groups of dentigerous lepidosaurs and crocodylians. This pattern of increasing dental complexity is consistent with similar patterns in both extinct and extant mammals (Evans et al., 2007; Boyer et al., 2010; Bunn et al., 2011; Santana et al., 2011; Godfrey et al., 2012; Wilson et al., 2012; Evans and Janis, 2014).

In contrast, the relationship between diet and tooth complexity is less pronounced than that observed in mammals, with significant overlap between all dietary categories in the midrange of tooth complexities (6–10 PPT at 25 RPT; Fig. 2.5B) although, to a lesser

extent, this complexity overlap is also found in extant mammals (Evans et al., 2007; Santana et al., 2011). Some herbivores examined in this study have relatively simple teeth, particularly *Uromastyx aegyptia*, *Egernia stokesii*, and *Tiliqua rugosa* (Fig. 2.11A, B). Why these animals possess simple dentition, whereas other herbivores have much more complicated morphologies, is unknown. Possible explanations may be the type of plant material they consume, phylogenetic history, or other constraints such as jaw motion.

Although lepidosaurs reduce their food using repeated bites, they do not masticate (Schwenk, 2000). In the case of *Uromastyx aegyptia* and *Iguana iguana*, small food items are swallowed whole, whereas larger, thin elements (e.g., leaves) are sheared (Throckmorton, 1976). Throckmorton (1976) hypothesized that cropping vegetation, as opposed to breaking it down, explains the dental morphology of *U. aegyptia* and *I. iguana*. Besides shearing plant material, little to no oral processing occurs (Throckmorton, 1976; Cooper and Vitt, 2002; Brizuela and Albino, 2009). The absence of mastication may be a possible explanation for the greater overlap between dietary categories and tooth complexity compared to mammals. Regardless of the differences in food processing compared with mammals, my results clearly demonstrate that dentigerous saurians who consume more plant material typically possess a more complex dentition.

Carnivores

Most carnivores measured possessed extremely simple dentitions. For example, *H. suspectum* and *V. varius* are similar in that they have recurved teeth with a high aspect ratio, but the dentition of *V. varius* is labiolingually compressed and more knife-like (Fig.

2.6). These knife-like teeth are useful in slicing flesh (Schwenk, 2000). In contrast, *G. gangeticus* is distinguished from the previous two dentitions by having relatively short, narrow, and sharp teeth. Carnivores with more complicated dentitions have conically shaped teeth in cross-section with a blunted apex (e.g., *Caiman crocodilus*, *Coluber constrictor*, and *Paleosuchus trigonatus*). These animals either swallow their prey whole if the item is small, or tear off large pieces, which are then swallowed without further processing (Cleuren and de Vree, 2000). The carnivorous lizard with the highest tooth complexity is *Crotaphytus bicinctores*, characterized by sharp, slightly recurved mesial teeth. McGuire (1996) reports that this species consumes a wide variety of food, including vertebrates (mainly lizards), a diverse selection of insects, and even a small amount of plant material. This higher level of insect material in addition to the plants may explain its slightly higher complexity given that insectivores generally have higher tooth complexity than generalist carnivores. Similarly, the diverse diet of other carnivores may account for their tooth complexity. In particular, many crocodylians (e.g., *Alligator mississippiensis*, *Caiman crocodilus*, *Crocodylus moreletii*, *Osteolaemus tetraspis*, *Paleosuchus trigonatus*) have extremely diverse diets (McNease and Joanen, 1977; Delany and Abercrombie, 1986; Tucker et al., 1996; Pauwels et al., 2003; Pauwels et al., 2007; Saalfeld et al., 2011; Laverty and Dobson, 2013), and this may be reflected in their somewhat high complexity, 5.23–6.8 PPT at 25 RPT. That being said, crocodylian tooth morphology also is, in part, controlled by the ability to resist extremely high bite forces (Erickson et al., 2012; Ősi, 2013).

Durophages

Both durophages in this study possess large, mesiodistally and labiolingually expanded teeth in the posterior portion of the jaw. These types of teeth are frequently cited as being used to crush hard-shelled organisms (Lönnberg, 1903; Conant, 1955; Edmund, 1969; Presch, 1974; Dalrymple, 1979; Rieppel and Labhardt, 1979; Estes and Williams, 1984; Losos and Greene, 1988). Because *Dracaena guianensis* and *Varanus niloticus* both possess fewer teeth than other carnivorous taxa, additional complexity is not a result of ancillary cusps, but from wider teeth (especially in *D. guianensis*) with small enamel ridges present near the center of the crown (Fig. 2.8).

Additionally, at high resolutions (50 RPT) small crenulations are detected by the OPCR analysis in *D. guianensis*, which increase the reconstructed complexity values (Fig. 2.8D). Rieppel and Labhardt (1979: Fig. 2.3B) figure and report this feature in *V. niloticus*, although they are not detected in this study, likely due to the wrinkles being covered by a thin layer of glue in the original specimen. It is suggested that these ridges help disperse pressure throughout the tooth and increase friction, preventing shells from slipping during crushing (Rieppel and Labhardt, 1979). Other teiids closely related to *Dracaena* have bulbous posterior teeth, such as the omnivorous *Tupinambis*, but these other taxa appear to lack crenulations (Fig. 2.10D; Dessem, 1985). Bulbous posterior teeth are relatively common in the amniote fossil record, particularly among crocodyliforms (Norell et al., 1994; Wu et al., 1996; Brochu, 1999; Ősi, 2013). This combination of morphological and complexity data suggests that, if the complexity values of an extinct amniote falls within or near the values of *D. guianensis* and *V. niloticus* and possesses small ridges or crenulations, that taxon was likely a durophage.

Insectivores

Insectivores exhibit a range of tooth complexities and morphologies, from simple unicuspid to tricuspid teeth (Fig. 2.9). This disparity is expected, because insects exhibit a wide range of physical properties and their predator's dental complexity has previously been shown to relate to the hardness of the consumed insects' exoskeleton (Hotton, 1955; Freeman, 1979; Strait, 1993; Evans and Sanson, 1998). There is a large degree of overlap in tooth complexities (OPCRavg and OPCRit) between insectivores and omnivores, a result similar to that observed in bats (Santana et al., 2011).

Insectivores with low average complexities (<8 PPT) are characterized by an homodont dentition (Fig. 2.9C). These teeth are usually unicuspid and cylindrical, although some can be slightly recurved (e.g., *Elgaria coerulea*). Acrodont insectivores in this study (e.g., *Chamaeleo senegalensis* and *Chamaeleo zeylanicus*) possess a distinct morphology from those of pleurodont lizards. Their teeth are labiolingually compressed, triangular in shape when viewed labially, and increase in size distally (Fig. 2.9A). Although the acrodont taxa possess a different morphology and implantation, their complexity values are similar to those of insectivorous with simple teeth. The ant-eating specialist *Moloch horridus* has relatively simple complexity values (6.23 PPT at 25 RPT), but this is a significant underestimate. The CT scan in this analysis does not satisfactorily capture the complex morphology exhibited in the distal-most dentary teeth (Bell et al., 2009).

Insectivorous saurians with higher complexities (>8 PPT) are heterodont and are typically characterized by a transition along the jaw from a simple unicusp incisiform tooth morphology to a tricusped morphology, with a large central cusp bordered by two

smaller cusps (Figs. 2.3, 2.9). These tricuspid teeth are typified by very little change in diameter from root to crown and a high tip-sharpness (Evans and Sanson, 1998). This general pattern is found throughout Squamata and is exemplified in *Basiliscus vittatus*, *Kentropyx pelviceps*, *Plica umbra*, and *Calotes mystaceus*.

Previous work on bats concluded that some aspects of dental morphology are related to the specific types of insects consumed (Freeman, 1979; Strait, 1993), but such a relationship is not apparent in saurians. Though any conclusions are preliminary because of limited detailed diet information in the literature, there does not seem to be a strong correlation between specific insectivore diets (e.g., a lizard that specializes in consuming a particular group of insects) and specific complexities. For example, Hotton (1955) suggested that a blunt, unicuspate, peg-like morphology, which would have a low complexity value, was indicative of an ant diet. This hypothesis is supported by two ant-eating specialists in this study, *Phrynosoma hernandesi* and *Sceloporus magister*, that have simple dentitions (7.98 and 8.88 PPT at 25 RPT, respectively). However, ant-eating specialist *Plica umbra* has a relatively high average dental complexity (10.9 PPT at 25 RPT), and another, *Moloch horridus*, would very likely have a high complexity value if the CT scans were higher resolution. The hypothesis that a simple morphology (and thus low tooth complexity) is correlated with an ant diet is therefore not supported by these data.

These data agree with Hotton (1955), who hypothesized that cuspate and sharp teeth are specialized for consuming active insects with a thicker integument (Presch, 1974). Both *Kentropyx pelviceps* and *Basiliscus vittatus* have diets comprised largely of grasshoppers (Hirth, 1963; Vitt et al., 1995). The tricuspate morphology of these taxa is

similar to the distal tooth morphology of *Gambelia sila*, which also consumes a large volume of active insects (e.g., grasshoppers; Hotton, 1955). Therefore, insectivorous lizards with high average tooth complexities (e.g., *Kentropyx*) specialize on insects that are more intractable, but lizards with low dental complexities eat insects with either hard or soft integuments. This discrepancy can be interpreted in a number of ways (although there are likely more explanations): 1) that simple, unicuspid lizard teeth are specialized for a wide dietary breadth; 2) there are other functional constraints influencing tooth complexity beyond diet, such as enamel thickness or continuous tooth replacement; 3) dietary data are incomplete for some of the sampled taxa (Cooper and Vitt, 2002); 4) phylogeny plays an important role in lizard dental morphology.

In insectivores, increased cusp number per tooth correlates with higher dental complexity values. This additional complexity may aid in breaking down tough insect cuticle. Although there is a distinct overlap in dental complexity values between insectivores and omnivores, the two diets can sometimes be distinguished based on a combination of complexity and discrete morphological characteristics. No insectivores measured in this study have more than three cusps. The cusps of insectivores generally have greater cusp sharpness relative to omnivores, which is expected, as sharper cusps require less force to penetrate tough insect exoskeletons (Evans and Sanson, 1998; Herrel et al., 2004). The hypothesis that sharp, triconodont teeth are indicative of a diet composed of insects with hard exoskeletons is thus supported by these data (Presch, 1974). Therefore, these data suggest that a combination both tooth morphology and complexity can be used to differentiate insectivores and omnivores in the amniote fossil record.

Omnivores

Similar to insectivores and herbivores, omnivorous saurians display a wide range of tooth complexities and morphologies, which is expected given the broad range of diets that omnivores consume (Evans et al., 2007). The simplest teeth of an omnivorous lepidosaur are found in *Varanus olivaceus*, which frequently, although highly selectively, consumes fruit (Auffenberg, 1988). Auffenberg (1988) described the dentary teeth of *V. olivaceus* in detail, with the mesial five or six teeth being cone-shaped and slightly recurved, whereas the distal teeth are blunted (lower tip sharpness). All teeth are nearly circular in cross-section (Auffenberg, 1988). He also described and figured fine striations on the distal maxillary and dentary of this animal, which are similar to those observed in durophagous lizards (Rieppel and Labhardt, 1979, and this study). Given that mollusks make up the majority of the animal material eaten by *V. olivaceus* (27.2% of total food items; Auffenberg, 1988), this is unsurprising and supports the hypothesis that these wrinkles are present on animals that consume a large amount of hard-shelled organisms, although the crenulations are so minute that they they are not recorded in even the most detailed OPCR analysis (50 RPT).

Omnivorous lizards express varying degrees of cusp development. *Acanthodactylus erythrurus* (7.87 PPT at 25 RPT) possesses a simple, unicuspid morphology, whereas *Gerrhosaurus* ("*Angolosaurus*") *skoogi* (10.48 PPT at 25 RPT), which has a diet in which plants make up over 80% of food consumed, has five cusps in the distal dentition (Pietruszka et al., 1986; Lamb et al., 2003; Nance, 2007). Such a high proportion of plant material in the diet is therefore consistent with a large number of cusps. The omnivores that possess multiple cusps on each tooth have cusp morphologies

that differ from those of most insectivores (Fig. 2.10). This is illustrated in the most complex omnivore dentitions: *Basiliscus plumifrons* (12.02 PPT at 25 RTP), *Teius teyou* (11.73 PPT at 25 RPT), and *G. skoogi* (10.48 PPT at 25 RPT). Each lizard possesses multiple cusps (2–5) per tooth that have a lower tip-sharpness (i.e., they are blunter) than what is observed in insectivorous saurians. This is not an artifact of different scan qualities (i.e., CT vs. μCT), as the three omnivores with the most complex teeth are from different scan sources (i.e., bone CT scan, bone μCT scan, and cast μCT scan). It is possible that this difference reflects the different properties and constraints of breaking down plant versus insect material.

In most cases, the increased complexity value results from an increased number of cusps, but some omnivores add complexity by labiolingually widening their teeth. Wider teeth increase complexity by generating a greater surface area for patches to be reconstructed, but it also allows for a more even distribution of patches already present (this is also the reason why conical teeth have more patches than laterally compressed teeth). *Teius teyou* labiolingually expands its distal teeth, as opposed to the labiolingually thin teeth of many herbivores (Fig. 2.14; Brizuela and Albino, 2009). This expansion is only observed in some teiids (e.g., *Dicrodon guttulatum* and *Dracaena guianensis*) and allows for larger and more circular cusps to develop. These cusps are taller and more prominent than those found in other omnivores and many herbivores.

Herbivores

On average, saurian herbivores possess the most complicated dentitions of any dietary category, but they also possess the largest range in dental complexities of any category (OPCRt, OPCRavg, and OPCRit at 25 RPT), partially overlapping with all other

dietary categories. This result was somewhat unexpected given that previous studies on extant mammals showed that nearly all herbivores have more complex teeth than carnivores (Evans et al., 2007; Santana et al., 2011). Even ignoring the two iguanids (*Cyclura carinata* and *Iguana iguana*; see above), and possibly a third (*Ctenosaura pectinata*), that have artificially low complexities because of resolution issues, the remaining herbivores with complexities below 9 PPT do have relatively simple dentitions. Simple teeth without accessory cusps typify the dentitions of *Egernia stokesii*, *Tiliqua rugosa*, and *Uromastyx aegyptia*, (Fig. 2.11; Cooper and Poole, 1973; Throckmorton, 1976; Hollenshead et al., 2011).

A number of potential explanations may account for this low complexity. Simple teeth may be a reflection of the parts of the plants or the specific plants they consume. For example, if these animals preferentially consume soft portions of plants, such as flowers and fruits, their teeth may not require the additional dental complexity (i.e., cusps) that other lizards have for breaking down tough vegetation. These three lizards have been documented to consume a variety of plant material, including leaves, fruits, flowers, and fungi (Brown, 1991; Foley et al., 1992; Cooper and Vitt, 2002). Their diets do not appear to constitute specific plant materials (e.g., flowers or fruits) that are softer or different from the material that other herbivorous lizards eat (Nagy, 1973; Iverson, 1979; Videla, 1983; Brown, 1991; Van Marken Lichtenbelt, 1993; Durtsche, 2000; Cooper and Vitt, 2002; Van Leeuwen et al., 2012). Additionally, previous research on the closely related species *T. multifasciata* and *T. occipitalis* found that variations in tooth morphology could not be correlated to dietary differences (Shea, 2006). Differences in the specific toughness of the plants that these taxa consume have not been tested and may

account for their relatively low complexity values.

It is possible that phylogenetic or developmental constraints may limit the tooth complexity of these three animals, but this is unlikely. In the case of *U. aegyptia,* other related nonherbivore agamids develop a complex (i.e., *Calotes mystaceus*) and/or heterodont dentition (i.e., *Moloch horridus*). Within Scincidae, a complex phenotype has evolved at least once in the possibly extinct omnivorous skink *Macroscincus coctei*. The dentition of this taxon is similar to that of many iguanids, with labiolingually compressed and cuspate crowns (Greer, 1976; Hutchinson, 1989; Cooper and Vitt, 2002). The development of moderately complex dentitions in both Agamidae and Scincidae suggests that developmental factors did not keep *Egernia, Tiliqua,* and *Uromastyx* from evolving more complex dentitions. The simple teeth of the herbivorous skinks could be a result of their recent evolutionary divergence from omnivorous or carnivorous skinks, but molecular divergence dates suggest this split occurred between 6.9 and 14.4 million years ago (Skinner et al., 2011; Hedges et al., 2015).

In most cases, herbivorous lepidosaurs do possess complex dentitions, which developed at least twice in disparate clades: Iguania and Teiidae (Figs. 2.13–14). Iguanid herbivores, including *Amblyrhynchus cristatus*, *Brachylophus fasciatus*, *Conolophus subcristatus*, *Dipsosaurus dorsalis*, *Phymaturus palluma*, and *Sauromalus ater*, have teeth with OPCRavg values above 10 PPT at 25 RPT. Similar to many omnivores, these teeth are labiolingually compressed and cuspate, though to varying degrees (Fig. 2.14). The single noniguanid herbivore with a high complexity value, *Dicrodon guttulatum*, developed a very different morphology, similar to its close relative, *Teius* (Brizuela and Albino, 2009). The dentary teeth of *D. guttulatum* are heterodont, with nine simple,

conical-shaped teeth followed by two transition teeth that possess a second cusp forming on the mesial margin of the tooth. The distal five teeth possess two labiolingually aligned cusps separated by a U-shaped depression, with the lingual cusp being approximately half the height of the labial (Presch, 1974). The cusps of the iguanid and teiid herbivores are both blunt, similar to the condition observed in omnivores.

Tooth Complexity, Diet, and Phylogeny

I performed a regression analysis to test for a potential correlation between OPCRavg and the volume of plant material in a dentigerous saurian's diet. This would allow me to determine if dental complexity increases as a direct result of increasing the volume of plant material in a diet. The regression does not explain a large amount of the variation, but it is significant ($R^2 = 0.18223$; Fig. S.2.2). I then conducted a phylogenetic independent contrasts test (pIC) for three different tree topologies (see Methods) to see if removing the effect of phylogeny would reveal a pattern between dental complexity and volume of plant material. pIC results for all three topologies display a low correlation between diet and tooth complexity after removing the effect phylogeny (Two tailed $P > 0.05$; Fig. S.2.3). The three *P*-values for the different topologies are similarly nonsignificant, demonstrating differences in the tree topologies do not significant change the results (Fig. S.2.3).

This low correlation between plant volume and dental complexity has a number of potential explanations. Each dietary category has a significant range in both OPCRavg and percent plant matter consumed (especially in omnivores), and this scatter may contribute to the low significance value. Additionally, insectivores often have high complexity values, even though many of them consume no plant material. The wide

variety of plant matter consumed by omnivores and herbivores may have an effect on dental complexity. The strong relationship between diet and tooth complexity, combined with a weak correlation between OPCRavg and the volume of plant material, indicates that the exact volume of plant material consumed is not controlling dental complexity; what appears to be more important is simply the presence/absence of plant material in the diet. Lastly, specific aspects of the plants consumed (e.g., toughness) may exert a measure of control on dental complexity, although this remains untested.

Implications for Reconstructing the Diet of Extinct Amniotes

This study demonstrates that tooth complexity and morphology correlate to diet in living saurians. In combination with recent studies on extant mammals (Evans et al., 2007; Santana et al., 2011; Godfrey et al., 2012), evidence suggests that diet strongly influences tooth morphology and complexity in amniotes, and therefore can be used to reconstruct the diet of extinct taxa, even those without living descendants or analogs (Wilson et al., 2012).

My results demonstrate that a combination of tooth complexity values and discrete dental traits should be employed when reconstructing the diet of extinct nonmammalian amniotes, because the range of dental complexity values for many dietary categories overlaps (between 6–8.5 PPT for all categories at 25 RPT). In addition to OPCRavg and OPCRit, key morphological traits such as cusp sharpness are useful.

Carnivores are diagnosed by a lower average tooth complexity (1–8 PPT at 25 RPT). Bulbous (mesiodistally and labiolingually expanded) teeth with distinct enamel crenulations and no additional cusps characterize durophages. The omnivorous *Varanus olivaceus* possesses teeth with wrinkled enamel, but this animal consumes hard-shelled

invertebrates for a large portion of its diet. When taken together, moderately complex dentitions (approximately 6–12 PPT at 25 RPT) with sharp cusps and a small jaw (<33 mm; Pough, 1973; Cooper and Vitt, 2002; but see Espinoza et al., 2004) suggests that an extinct amniote is an insectivore. On the other hand, an extinct amniote with moderately complex teeth, blunter teeth, and a larger jaw is likely an omnivore. Data from this study suggest that amniotes with high levels of dental complexity (>12.5 PPT OPCRavg and >15 PPT OPCRit at 25 RPT) are herbivores. At medium complexities (8.8–12.5 PPT for an OPCRavg analysis at 25 RPT) it will be difficult to confidently refer an extinct taxon to an herbivore, omnivore, or insectivore without additional morphological data. Taken together, these data suggest there is great potential for using OPCR to reconstruct the diet of a variety of extinct amniotes that do not have close living relatives (e.g., caseids, archosauromorphs, and extinct crocodyliforms; Maddin et al., 2008; Flynn et al., 2010; Kley et al., 2010).

Conclusions

It has been suggested for over 60 years that diet and tooth complexity of extant lizards are positively correlated, but these previous studies have only used qualitative methods on isolated clades (Hotton, 1955; Montanucci, 1968; Presch, 1974; Mateo and López-Jurado, 1992; Barrett, 2000; Cooper and Vitt, 2002). This is the first study to use a homology-free, quantitative technique, orientation patch count rotated (OPCR), to analyze the phenotypic morphology and complexity in representatives from all major dentigerous clades of extant saurians. All analyses of dental complexity show a clear gradation from low complexity (simple teeth) in carnivores to high complexity values in herbivorous saurians. Therefore, similar to living and extinct mammals, diet correlates

with phenotypic tooth complexity in living saurians (Evans et al., 2007; Santana et al., 2011; Godfrey et al., 2012; Evans and Janis, 2014). Additionally, some discrete dental characters can help distinguish between dietary categories when they have overlapping complexity values. Therefore, OPCR, when combined with additional morphological data, has the potential to be used to reconstruct the diet, and potentially other aspects of paleoecology, of extinct amniotes.

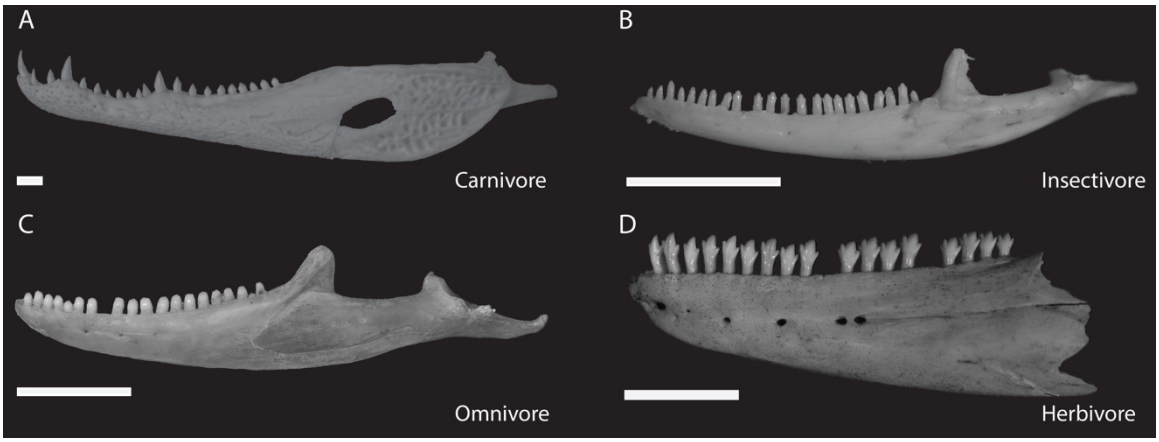


Figure 2.1- Comparisons of four saurian left dentaries from a range of wide range of clades and diets: **A**) *Paleosuchus trigonatus* (USNM 300660); **B**) *Laemanctus longipes* (UCMP 129880); and **C**) *Gerrhosaurus major* (UCMP 137878); **D**) *Conolophus subcristatus* (UCMP 68040). Note the significant variation in dental morphology. Scale bars equal 1 cm. Abbreviations: **UCMP,** University of California Museum of Paleontology; **USNM**, National Museum of Natural History.

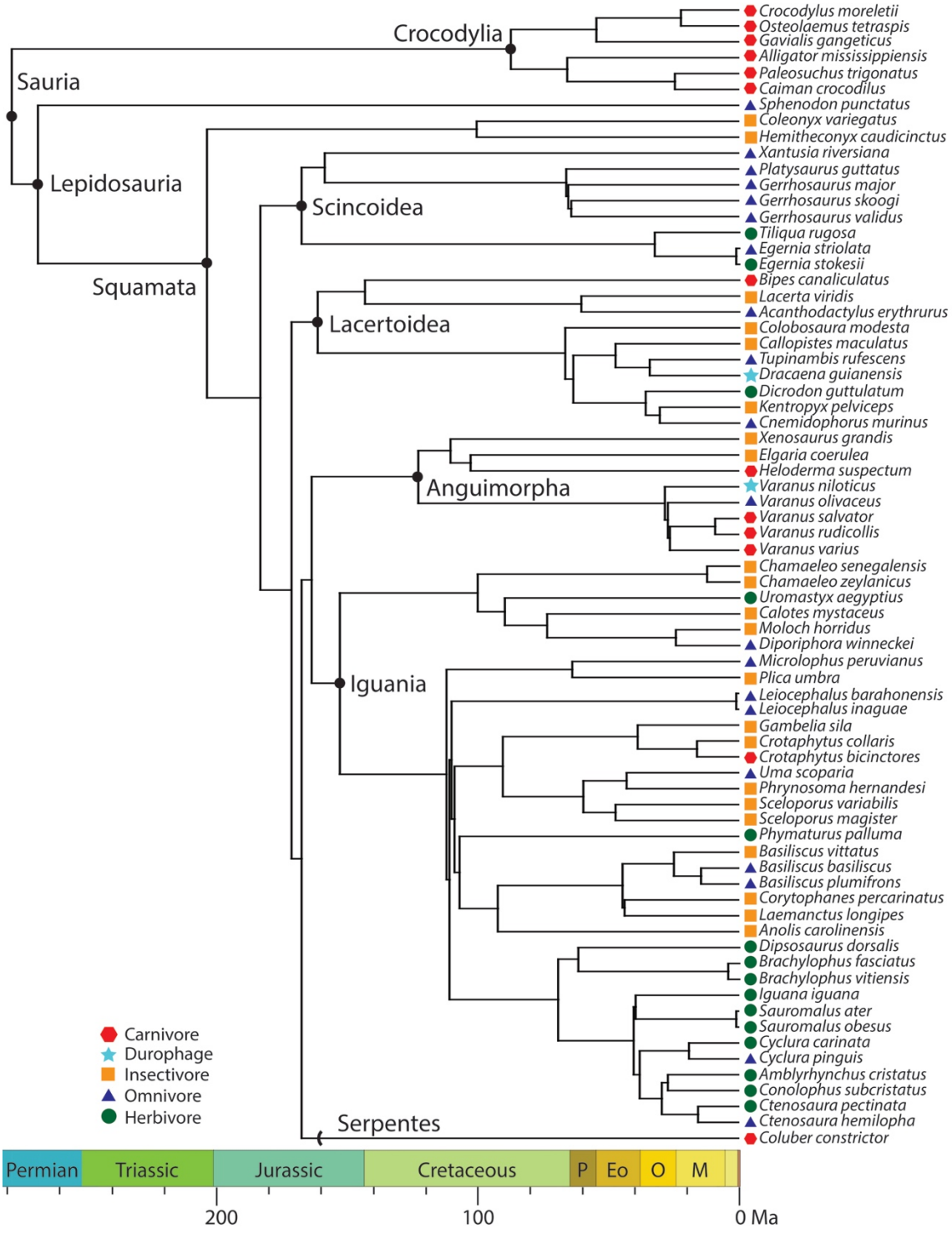


Figure 2.2- Time-calibrated phylogeny illustrating the relationships and diet of most saurian taxa included in this study. Tree topology is taken from Pyron et al. (2013) and divergence ages are from Hedges et al. (2015).

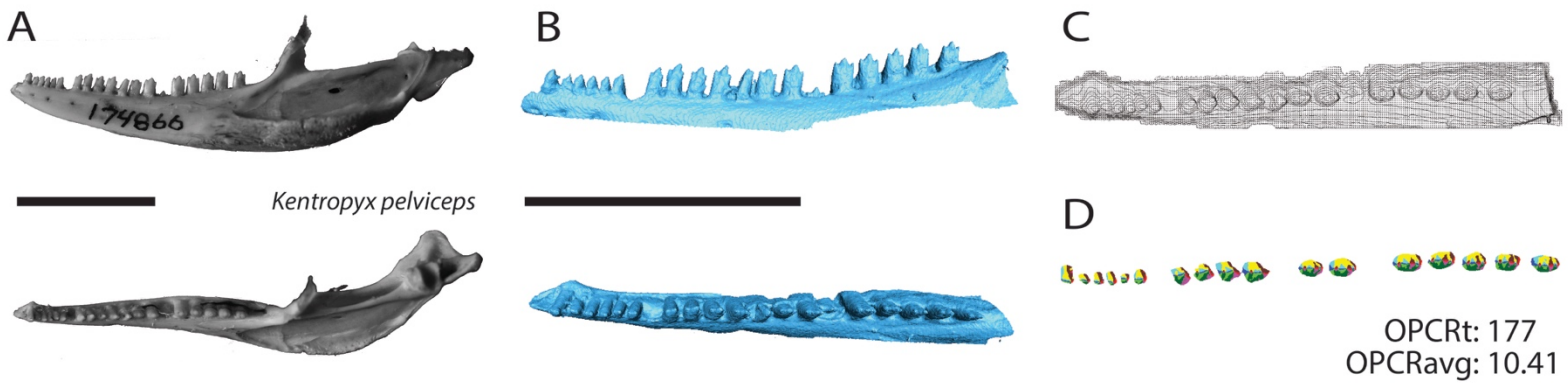


Figure 2.3- The left dentary of *Kentropyx pelviceps* (MVZ 174866) illustrating the steps for analyzing dental complexity using orientation patch count rotated (OPCR). **A**) Lateral and occlusal (top down) view of the lower jaw. **B)** Edited 3D surface model in lateral (top) and occlusal (bottom) view of the left dentary with most of the dentary removed. **C**) Contour map of the tooth row in occlusal view. **D)** OPCR surface orientation map of the tooth row in occlusal view. Scale bar equals 1 cm. Abbreviation: **MVZ,** Museum of Vertebrate Zoology at Berkeley.

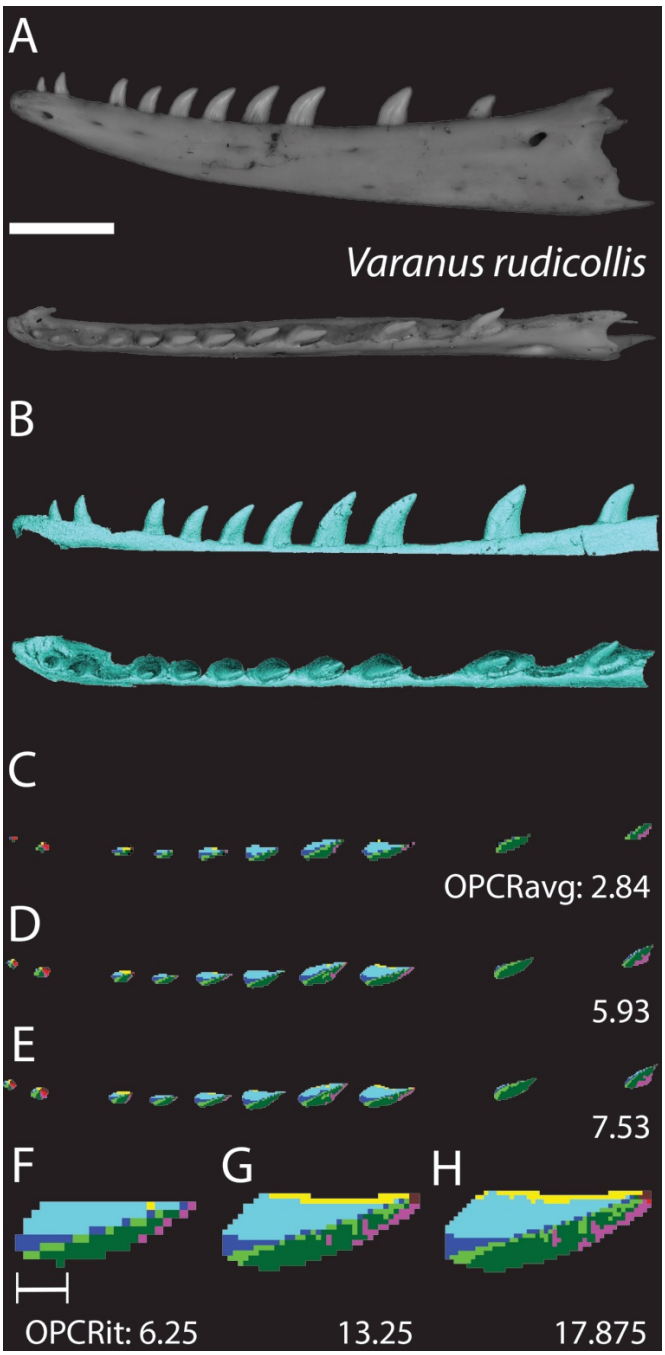


Figure 2.4- Analysis of OPCR results for a specimen of the carnivore *Varanus rudicollis* (UCMP 137816). **A)** Left dentary in lateral and occlusal view. **B)** Surface model of the same specimen in lateral and occlusal view. OPCR orientation maps analysis of full jaw at 25 data rows per tooth (RPT) **C)**, 40 RPT **D)**, and 50 RPT **E)**. Enlargement of a single tooth from the OPCR analysis at 25 RPT **F)**, 40 RPT **G)**, and 50 RPT **H)**. As the number of data rows per tooth increases in the analysis, the level of detail and measured complexity increase. Scale bar for **A**–**E** equals 1 cm. Scale bar for **F**–**H** equals 1 mm. Abbreviation: **UCMP,** University of California Museum of Paleontology.

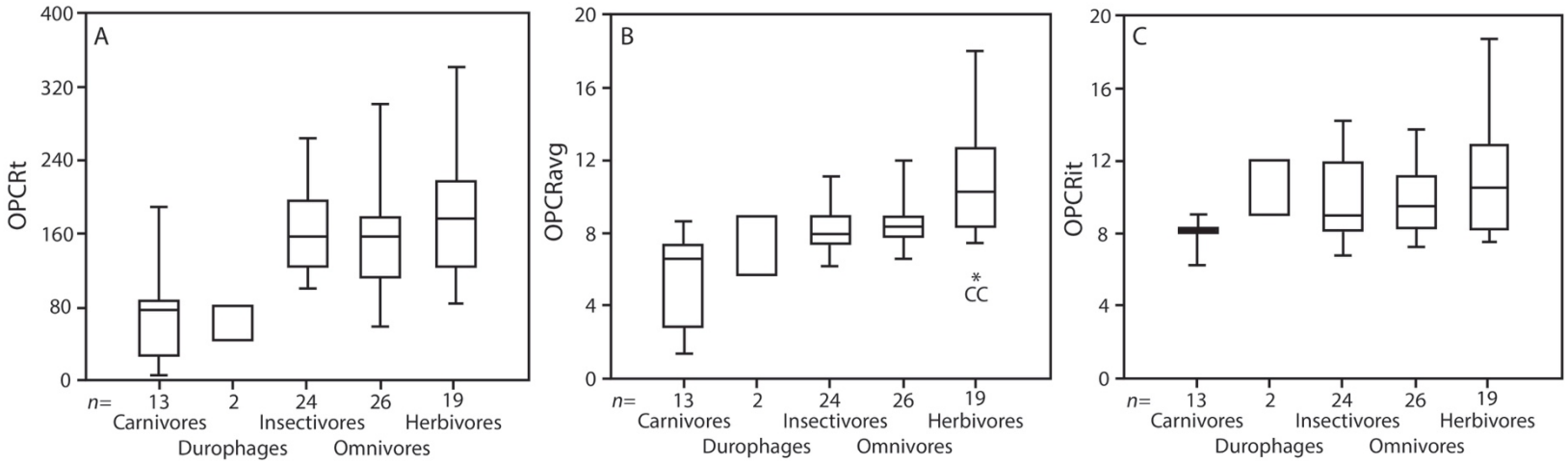


Figure 2.5- Observed range of tooth complexity (OPCR) for the five measured dietary categories. **A**) OPCRt for the entire jaw at 25 RPT; **B**) OPCRavg at 25 RPT. One outlier, the iguanid *Cyclura carinata*, is denoted with an asterisk; **C)** Phenotypic complexity of isolated teeth (OPCRit) at 25 RPT. Boxes encompass 25–75 percent quartiles. The median is designated by a horizontal line. The minimum and maximum values are shown with short horizontal lines. *n* represents the number of species in each dietary category.

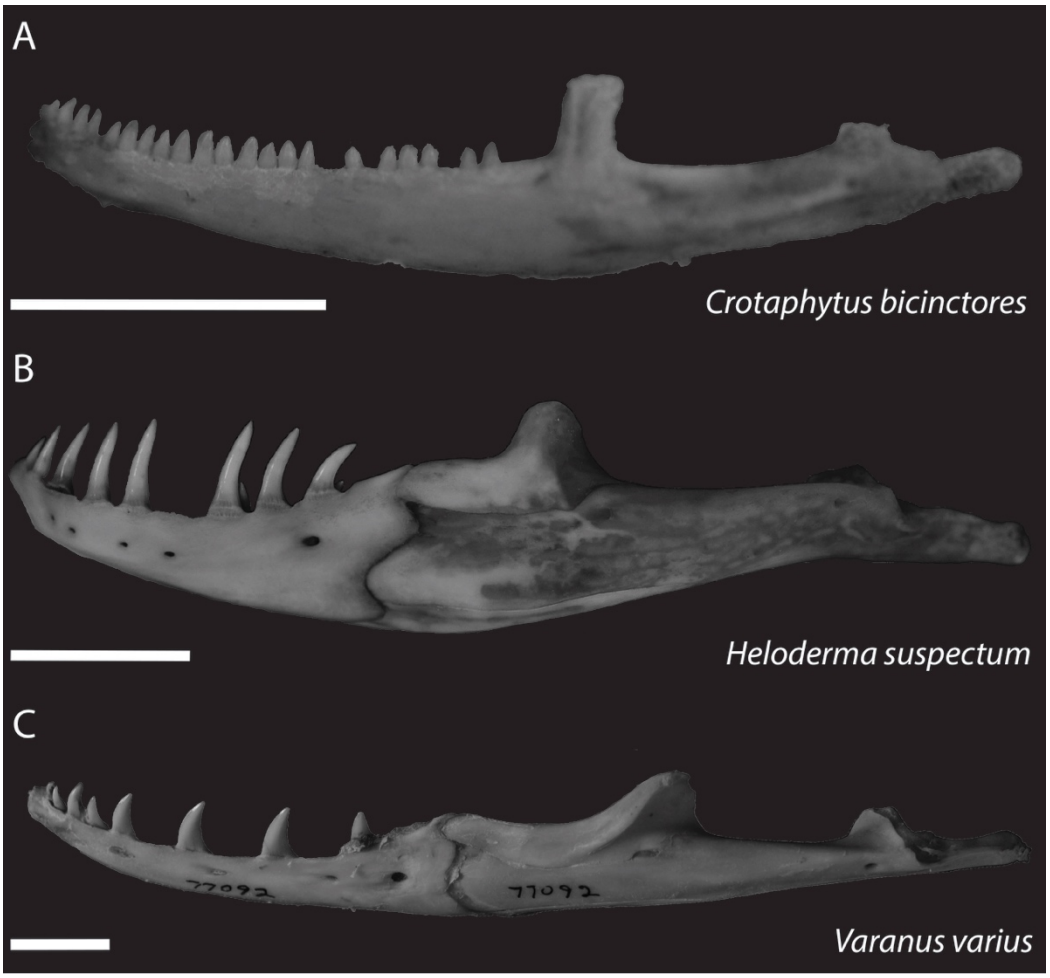


Figure 2.6- Examples of left dentaries (lateral view) from carnivorous taxa illustrating the disparity in tooth morphology. The iguanian **(A)** *Crotaphytus bicinctores* (CAS 200859) possesses a large number of small, peg-like teeth, whereas the anguimorphs **(B)** *Heloderma suspectum* (CAS 159492) and **(C)** *Varanus varius* (MVZ 77092) have fewer, large recurved teeth. Scale bar equals 1 cm. Abbreviations: **CAS,** California Academy of Sciences; **MVZ,** Museum of Vertebrate Zoology at Berkeley.

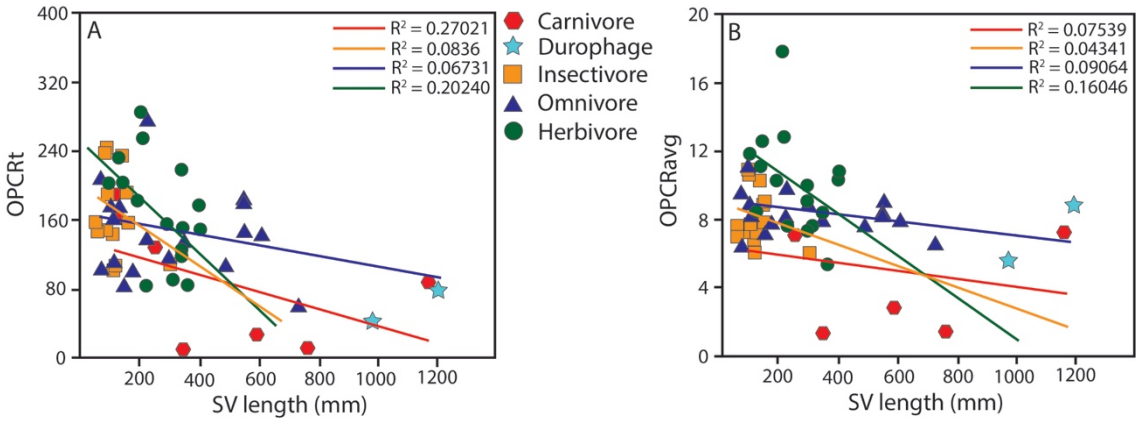


Figure 2.7- Graphs illustrating the poor relationship between maximum snout-vent [SV] length and OPCRt **(A)** and OPCRavg **(B)**. Only taxa with reliable body size information were included. Crocodylians were not included. Trend line color corresponds to diet. Durophage trend line was not included because there are only two points.

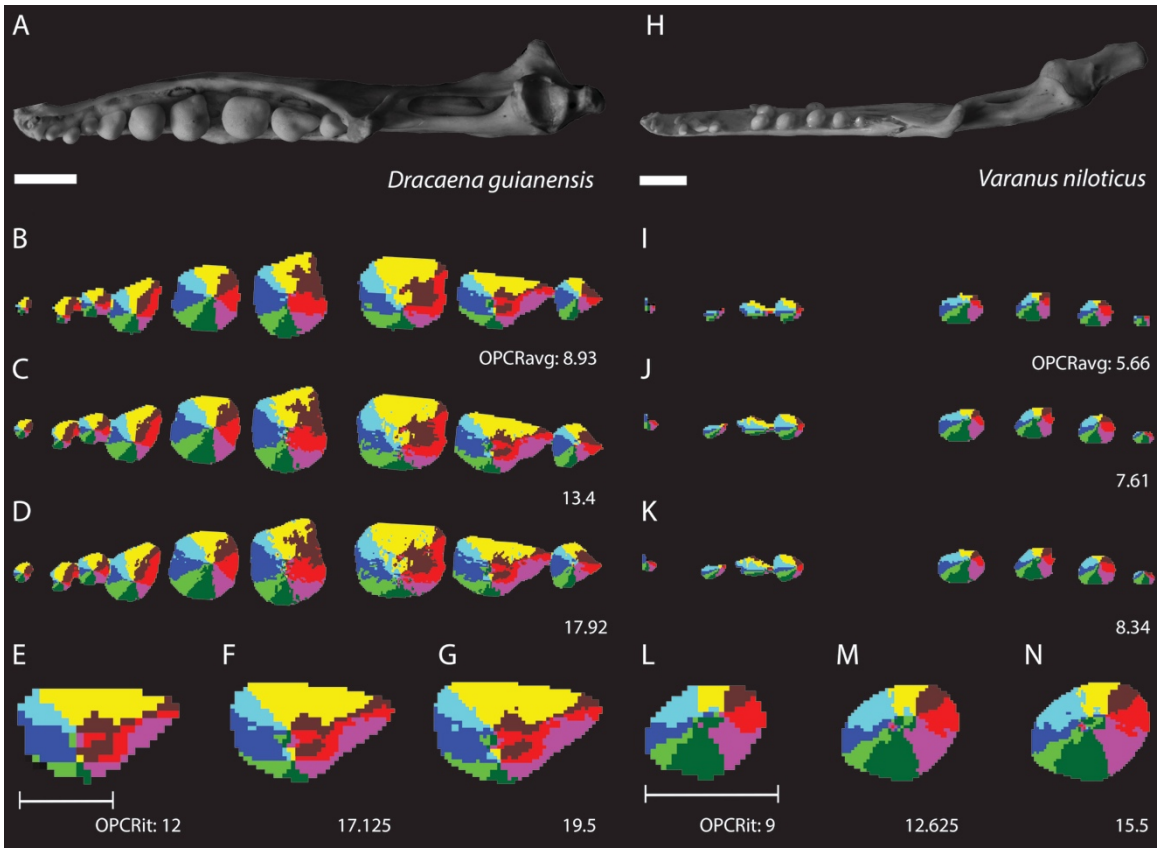


Figure 2.8- Dental complexity of durophagous taxa *Dracaena guianensis* (MVZ 79247) and *Varanus niloticus* (MVZ 68534). Photos of the left dentary in occlusal view (**A** and **H**); OPCR orientation maps for the entire tooth row at 25 (**B** and **I**), 40 (**C** and **J**), and 50 (**D** and **K**) RPT; and OPCR orientation maps for a single tooth at 25 (**E** and **L**), 40 (**F** and **M**), and 50 (**G** and **N**) RPT. Note the surface wrinkled texture of the teeth apparent in the orientation maps for *Dracaena*. Jaw photos are from lateral view, whereas orientation maps are from occlusal view. Top scale bars for **A**–**D**, **H**–**K** equal 1 cm. Line scale bars for **E**–**G**, **L**–**N** equal 5 mm. Abbreviation: **MVZ,** Museum of Vertebrate Zoology at Berkeley.

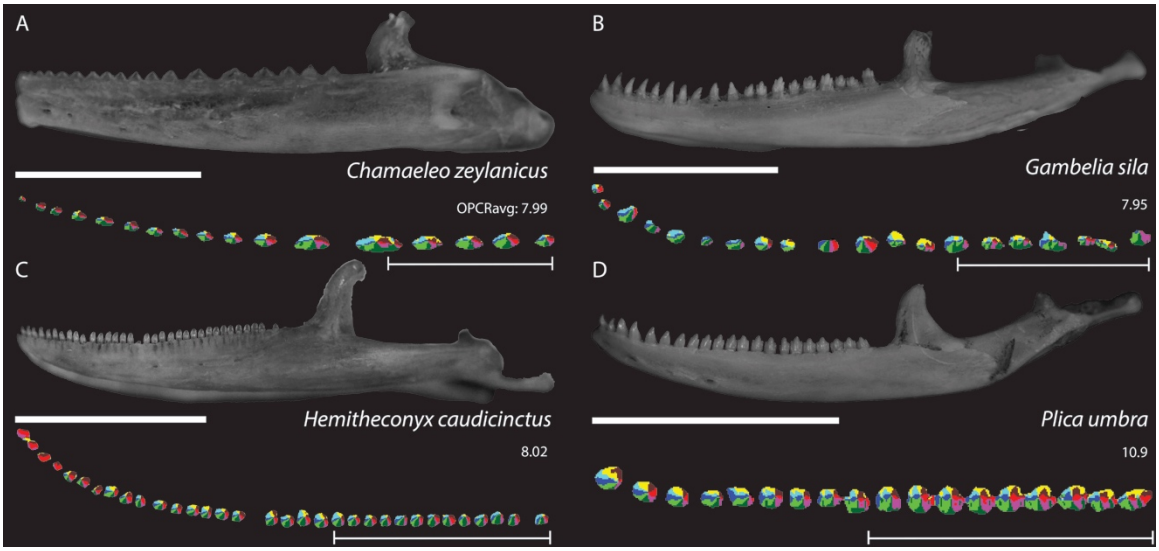


Figure 2.9- A selection of dentaries in lateral view from insectivorous taxa illustrating the disparity in tooth morphology. The iguanids **(A)** *Chamaeleo zeylanicus* (CAS uncatalogued) and **(B)** *Gambelia sila* (CAS 141318) and the gekkotan **(C)** *Hemitheconyx caudicinctus* (CAS uncatalogued) possess relatively simple teeth, whereas the teiid **(D)** *Plica umbra* (CAS 93242) has a much more complex dentition. OPCR maps in occlusal view are below the photos of each specimen. Scale bar below photos equals 1 cm. Line scale bars below OPCR maps equals 5 mm. Abbreviation: **CAS,** California Academy of Sciences.

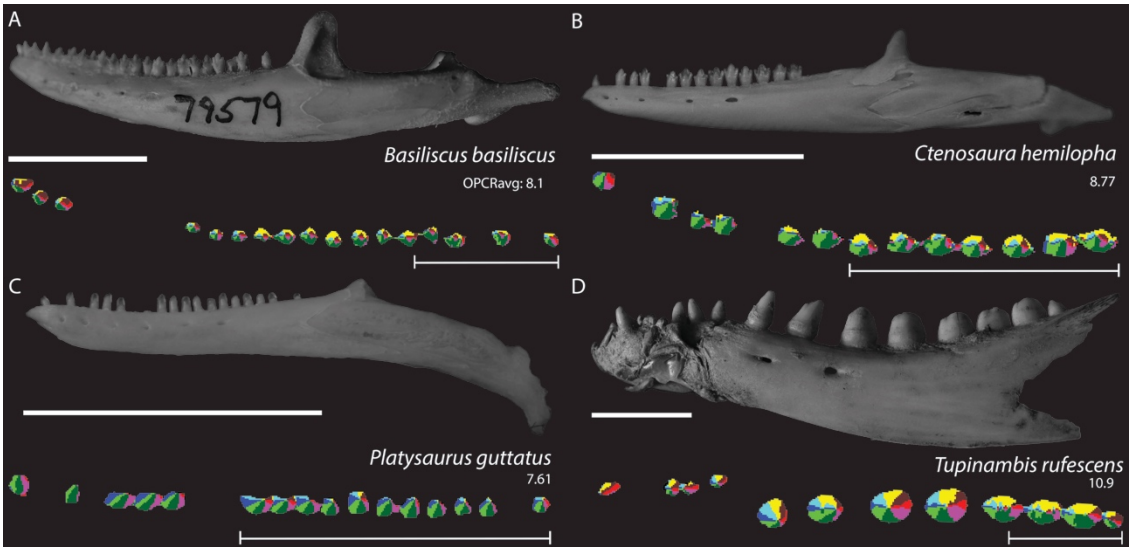


Figure 2.10- A selection of dentaries in lateral view from omnivorous taxa illustrating the disparity in tooth morphology. Note the tricuspate morphologies of the iguanids **(A)** *Basiliscus basiliscus* (MVZ 79579) and **(B)** *Ctenosaura hemilopha* (CAS 46399) compared to the smaller, peg-like teeth of the skink **(C)** *Platysaurus guttatus* (MCZ R-44415) and the wide teeth of the teiid **(D)** *Tupinambis rufescens* (MVZ 92987) OPCR maps in occlusal view are below the photos of each specimen. Scale bars below the photos equal 1 cm. Line scale bars below OPCR maps equal 5 mm. Abbreviations: **CAS,** California Academy of Sciences; **MCZ-R,** Museum of Comparative Zoology, Harvard University; **MVZ,** Museum of Vertebrate Zoology at Berkeley.

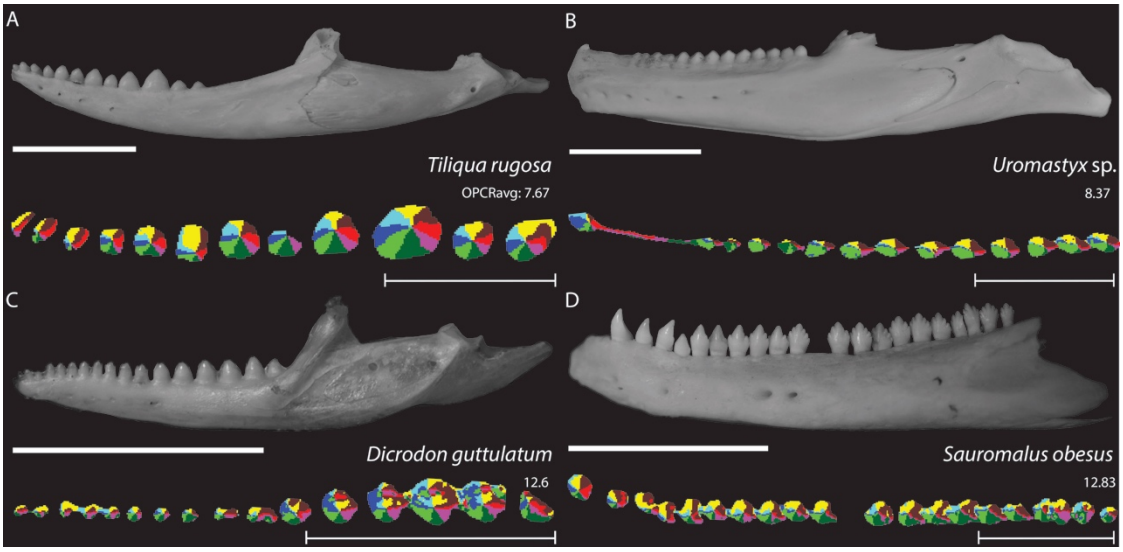


Figure 2.11- A selection of dentaries in lateral view from an herbivorous **(A)** skink (MCZ R-24456), **(B)** agamid (UCMP 118912), **(C)** teiid (MVZ 85400), and **(D)** iguanid (UCMP 137811) illustrating the disparity in tooth morphology. OPCR maps in occlusal view are below the photos of each specimen. Note the wide variation in tooth size, shape, and complexity in herbivorous lizards. Scale bar below photos equals 1 cm. Line scale bars below OPCR maps equals 5 mm. Abbreviations: **MCZ-R,** Museum of Comparative Zoology, Harvard University; **MVZ,** Museum of Vertebrate Zoology at Berkeley; **UCMP,** University of California Museum of Paleontology.

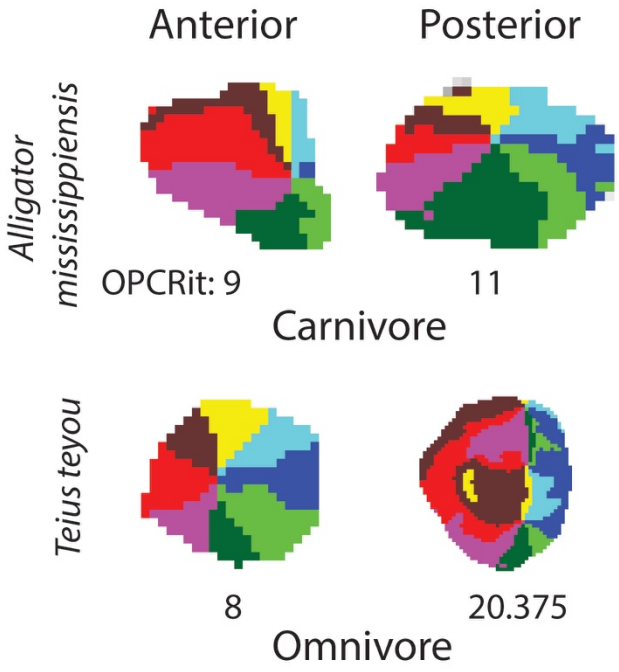
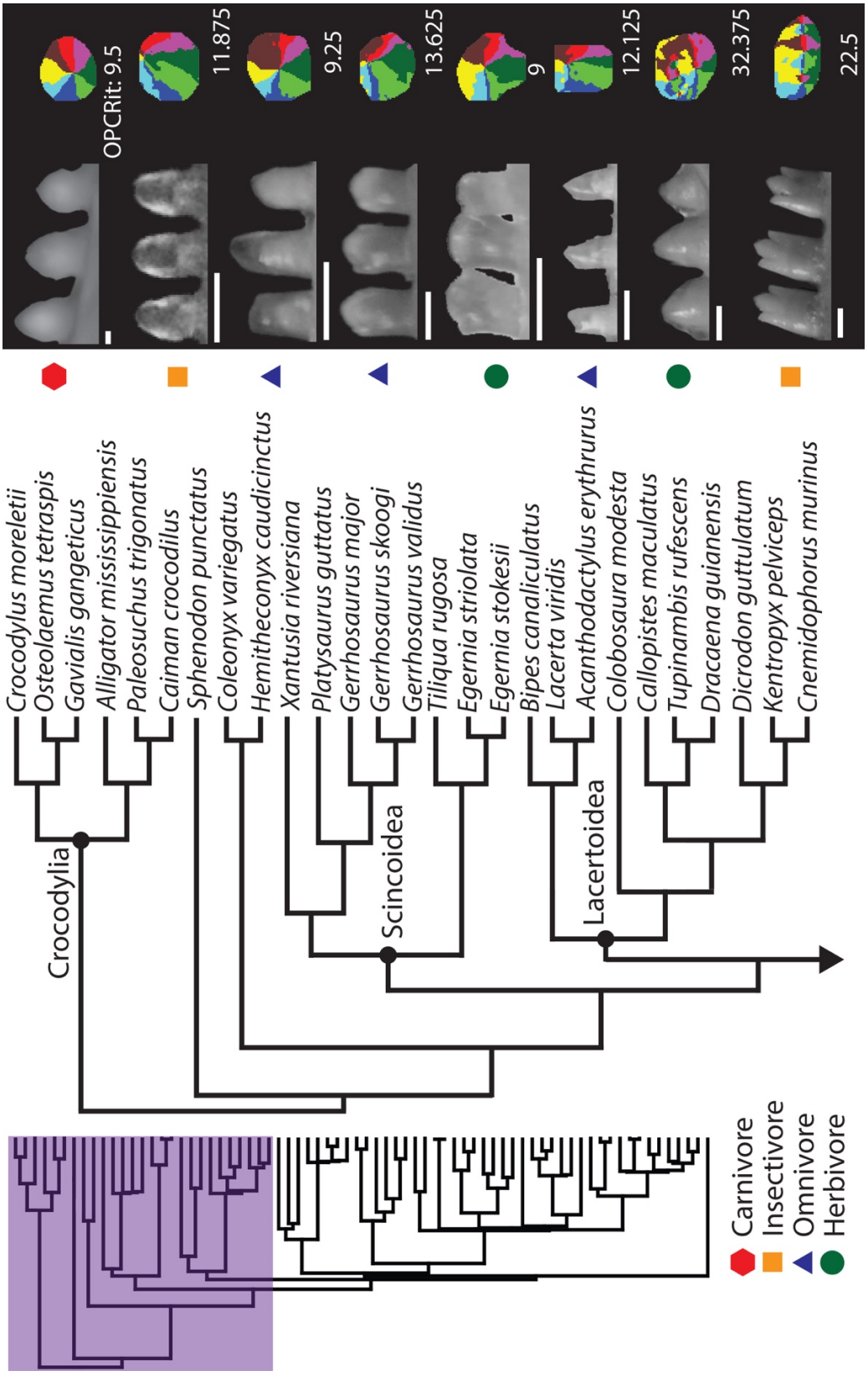


Figure 2.12- OPCR orientation maps showing the difference between the individual teeth of a carnivore, *Alligator mississippiensis*, and omnivore, *Teius teyou*. Note how anterior, incisiform teeth are significantly simpler than posterior teeth in the omnivore, whereas the complexities are similar in the carnivore.

Figure 2.13- Phylogenetic distribution of diet in comparison to tooth complexity for taxa in this study. Pictures of three posterior teeth (lateral view) and orientation maps of isolated teeth (occlusal view) of select taxa are included to illustrate the dental disparity between Crocodylia, Scincoidea, and Lacertoidea (from top to bottom: *Paleosuchus trigonatus* USNM 300660, *Hemitheconyx caudicinctus* CAS uncatalogued, *Platysaurus guttatus* MCZ R-44415, *Gerrhosaurus validus* MCZ R-50973, *Egernia stokesii* MCZ R-33105, *Acanthodactylus erythrurus* SDNHM 65166, *Dicrodon guttulatum* MVZ 85400, and *Kentropyx pelviceps* MVZ 77092). Phylogeny modified from Pyron et al. (2013). Scale bars equal .5 mm. Abbreviations: **CAS,** California Academy of Sciences; **MCZ-R,** Museum of Comparative Zoology, Harvard University; **MVZ,** Museum of Vertebrate Zoology at Berkeley; **SDNHM**, San Diego Natural History Museum; **USNM**, National Museum of Natural History.


OPCRit: 9.5
11.875
9.25
13.625
9
12.125
32.375
22.5
Crocodylus moreletii
Osteolaemus tetraspis
Gavialis gangeticus
Alligator mississippiensis
Paleosuchus trigonatus
Caiman crocodilus
Sphenodon punctatus
Coleonyx variegatus
Hemitheconyx caudicinctus
Xantusia riversiana
Platysaurus guttatus
Gerrhosaurus major
Gerrhosaurus skoogi
Gerrhosaurus validus
Tiliqua rugosa
Egernia striolata
Egernia stokesii
Bipes canaliculatus
Lacerta viridis
Acanthodactylus erythrurus
Colobosaura modesta
Callopistes maculatus
Tupinambis rufescens
Dracaena guianensis
Dicrodon guttulatum
Kentropyx pelviceps
Cnemidophorus murinus
Crocodylia
Scincoidea
Lacertoidea
Carnivore
Insectivore
Omnivore
Herbivore

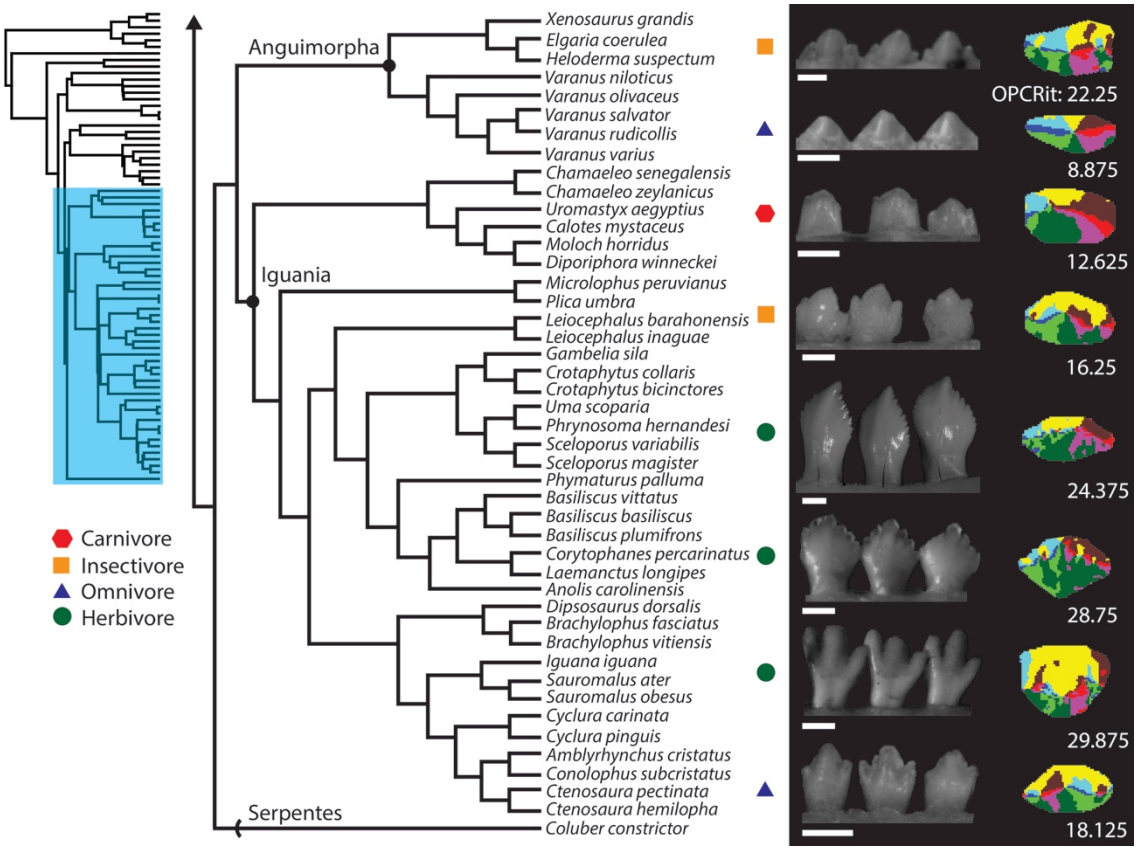


Figure 2.14- Phylogenetic relationships and dietary habits of the Iguania, Anguimorpha, and Serpentes. Pictures of three teeth from the left dentaries (lateral view) and orientation maps of isolated teeth (occlusal view) of select taxa are included to illustrate the dental diversity within this clade (from top to bottom: *Calotes mystaceus* CAS 243761, *Diporiphora winneckei* MCZ R-35222, *Crotaphytus bicinctores* CAS 65217, *Corytophanes percarinatus* UCMP 123057, *Iguana iguana* UMNH 8084, *Sauromalus ater* MVZ 100404, *Amblyrhynchus cristatus* MVZ 67721, and *Ctenosaura hemilopha* CAS 46399). Phylogeny modified from Pyron et al. (2013). Scale bars equal .5 mm. Abbreviations: **CAS,** California Academy of Sciences; **MCZ-R,** Museum of Comparative Zoology, Harvard University; **MVZ,** Museum of Vertebrate Zoology at Berkeley; **UCMP,** University of California Museum of Paleontology; **UMNH,** Natural History Museum of Utah.

Table 2.1- Dietary information (category and percentage of diet composed of plant material, when available), and OPCRt values of taxa measured in this study. Quantitative dietary data are often unavailable or sometimes incompatible. I chose to use volumetric data from the contents of the digestive tract following that of Cooper and Vitt (2002). When reliable dietary information was not available the cell is marked with a '?'. ~ denotes an approximation of plant volume in diet.

Name	Diet	% Plants in diet	Number of Teeth	OPCRt at 25 RPT
Acanthodactylus erythrurus	Omnivore	65.5	19	149.500
Alligator mississippiensis	Carnivore	<10	17	88.875
Amblyrhynchus cristatus	Herbivore	100	19	342.625
A. cristatus (UCMP 137167)	Herbivore	100	12	167.375
Amphiglossus splendidus	Insectivore	0	16	128.750
Anolis carolinensis	Insectivore	0	21	151.875
Basiliscus basiliscus	Omnivore	22	28	274.750
B. basiliscus (MVZ 79579)	Omnivore	22	17	137.750
Basiliscus vittatus	Insectivore	8.76	22	244.750
Basiliscus plumifrons	Omnivore	27.64	25	300.375
Bipes canaliculatus	Carnivore	0	6	49.625
Brachylophus fasciatus	Herbivore	~90	18	184.375
Brachylophus vitiensis	Herbivore	100	11	84.375
Caiman crocodilus	Carnivore	<10	17	115.750
Callopistes maculatus	Insectivore	0	13	100.250
Calotes mystaceus	Insectivore	0	17	241.375
Chalarodon madagascariensis	Omnivore	~25.85	24	206.500
Chamaeleo senegalensis	Insectivore	0	18	112.750
Chamaeleo zeylanicus	Insectivore	0	17	135.750
Cnemidophorus murinus	Omnivore	76	8	64.875
Coleonyx variegatus	Insectivore	0	33	243.125
Colobosaura modesta	Insectivore	0	25	195.000
Coluber constrictor	Carnivore	0	10	75.375
Conolophus subcristatus	Herbivore	98	17	177.875
C. subcristatus (Right Maxilla)	Herbivore	98	14	150.375
Corytophanes percarinatus	Insectivore	0	16	123.250
Crocodylus moreletii	Carnivore	<10	12	78.375
Crotaphytus bicinctores	Carnivore	0	22	190.375
Crotaphytus collaris	Insectivore	<10	15	111.250
Ctenosaura pectinata	Herbivore	100	21	155.625
Ctenosaura hemilopha	Omnivore	86.4	13	114.000
Cyclura carinata	Herbivore	>95	16	91.125

Table 2.1- Continued

Name	Diet	% Plants in diet	Number of Teeth	OPCRt at 25 RPT
Cyclura pinguis	Omnivore	71	22	182.875
Dicrodon guttulatum	Herbivore	~90	16	201.875
Diporiphora winneckei	Omnivore	27.5	10	89.500
Dipsosaurus dorsalis	Herbivore	97.3	21	235.000
Dracaena guianensis	Molluscivore	0	9	80.375
Egernia striolata	Omnivore	39.7	19	160.125
Egernia stokesii	Herbivore	96.15	21	179.000
Elgaria coerulea	Insectivore	<10	21	147.500
Gambelia sila	Insectivore	<10	20	159.000
Gavialis gangeticus	Carnivore	0	19	24.875
Gerrhosaurus major	Omnivore	11	18	148.500
G. major (CAS 204767)	Omnivore	11	20	179.750
Gerrhosaurus skoogi	Omnivore	82.6	15	157.250
Gerrhosaurus validus	Omnivore	72	20	156.500
Heloderma suspectum	Carnivore	0	5	6.625
Hemitheconyx caudicinctus	Insectivore	0	33	264.500
Iguana iguana	Herbivore	100	17	156.500
I. iguana (UCMP 123051)	Herbivore	100	22	220.375
Intellagama lesueurii	Insectivore	~50	18	128.500
Kentropyx pelviceps	Insectivore	0	17	177.000
Lacerta viridis	Insectivore	0	20	161.375
Laemanctus longipes	Insectivore	0	22	198.250
Leiocephalus barahonensis	Omnivore	<10	22	220.370
Leiocephalus inaguae	Omnivore	24.9	20	162.625
Leiolepis belliana	Omnivore	~25	12	85.750
Microlophus peruvianus	Omnivore	10.9	20	174.625
Moloch horridus	Insectivore	0	17	105.875
Osteolaemus tetraspis	Carnivore	<10	13	83.375
Paleosuchus trigonatus	Carnivore	<10	21	151.000
Phrynosoma hernandesi	Insectivore	0	19	151.750
Phymaturus palluma	Herbivore	100	17	203.000
Platysaurus guttatus	Omnivore	78	16	121.750
Plica umbra	Insectivore	0	18	196.250
Sauromalus ater	Herbivore	99	16	215.625
Sauromalus obesus	Herbivore	100	20	256.500
Sceloporus magister	Insectivore	5	27	239.875
Sceloporus variabilis	Insectivore	0	21	162.000

Table 2.1- Continued

Name	Diet	% Plants in diet	Number of Teeth	OPCRt at 25 RPT
Sphenodon punctatus	Omnivore	14	18	142.625
Teius teyou	Omnivore	~80	15	176.000
Tiliqua rugosa	Herbivore	93.7	12	92.000
Tupinambis rufescens	Omnivore	36.7	14	107.125
Tupinambis teguixin	Omnivore	~50	17	133.875
Uma scoparia	Omnivore	13.3	20	162.875
Uromastyx aegyptia	Herbivore	100	14	118.250
Uromastyx sp.	Herbivore	100	15	125.500
Varanus niloticus	Molluscivore	0	8	45.250
Varanus olivaceus	Omnivore	55	9	59.625
Varanus rudicollis	Carnivore	0	10	28.375
Varanus salvator	Carnivore	0	12	87.875
Varanus varius	Carnivore	0	7	9.750
Xantusia riversiana	Omnivore	18.7	13	109.000
Xenosaurus grandis	Insectivore	2.24	20	160.875

Appendix

Molding Procedure

The molding procedure is as follows. First, the dentary was partially covered by a wetted, thin piece of paper. This layer ensured the molding material would not imbue into the small foramen, which may damage the bone or mold when the material is removed. Reprosil light body catalyst and base molding material were then combined at a one-to-one ratio and applied to the wetted paper, bones, and teeth. The mixture was then allowed to set for approximately 10 minutes. Typically, two or more layers of molding material were applied to each tooth row to ensure that the molds would not tear when removed. For small jaws, the dentary was placed upside down in a small pool of molding material. Before casting at the NHMU, an additional layer of molding material was added to increase the depth and thickness of the mold, which prevented overflow of the casting resin and increased durability and resistance to tearing, respectively.

Casts were made using EPOTEK 301 epoxy resin, which has submicron resolution (Teaford and Oyen, 1989). A small volume of resin was added to each mold, enough to fill in every tooth in the jaw, stopping at the dorsal edge of the dentary. The molds were then placed in a vacuum chamber for approximately 5 minutes to remove any large bubbles from the casting resin. The resin was then allowed to cure for two days before a second layer of casting material was added. The second layer thickened and strengthened the casts. The casts cured for an additional two days before they were removed from the molds. In many cases the molds were undamaged when the casts were removed. If damage did occur, the most common issue was the base of the mold tearing, although this did not damage the tooth morphology. Very rarely the molding material

between two closely set teeth would be torn out upon cast removal, permanently damaging the mold, but this never affected more than two teeth in a single mold.

Supplemental Figures

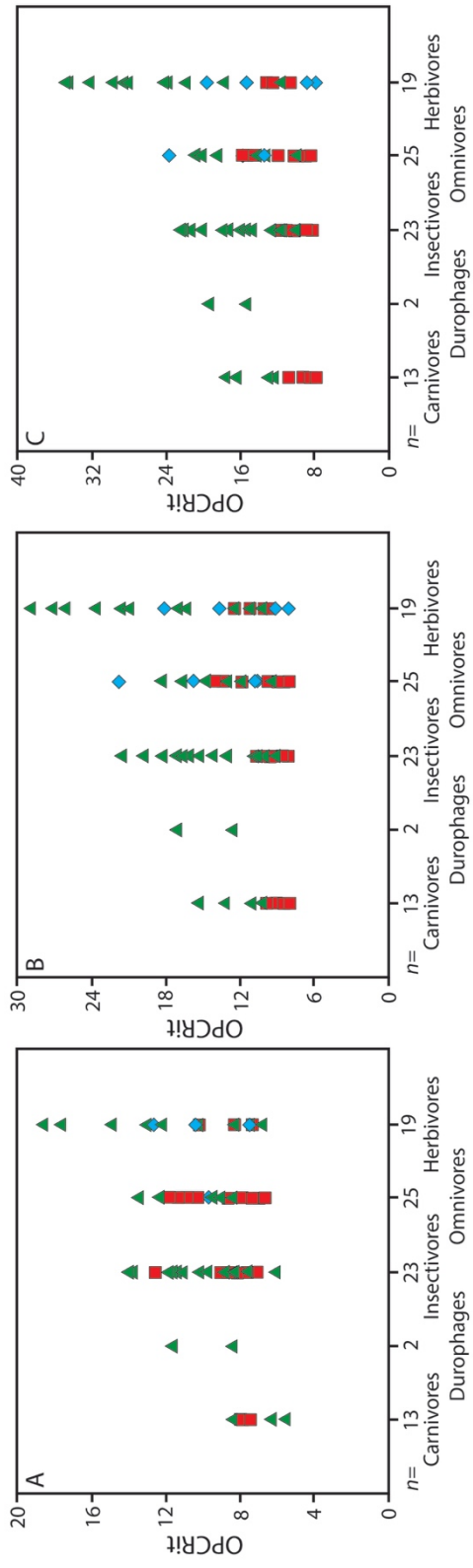


Figure S.2.1- Orientation patch count rotated of individual teeth (OPCRit) at 25 **(A)**, 40 **(B)**, and 50 **(C)** data rows per tooth. Red squares indicate Digimorph CT scans, green triangles represent µCT scans of casts, whereas the blue diamonds show µCT scans of bones. Note how the µCT scans of casts become concentrated in the higher complexity values for each dietary category in B and C. Because of this separation, 25 RPT is the preferred resolution to analyze CT and µCT scan data with OPCR.

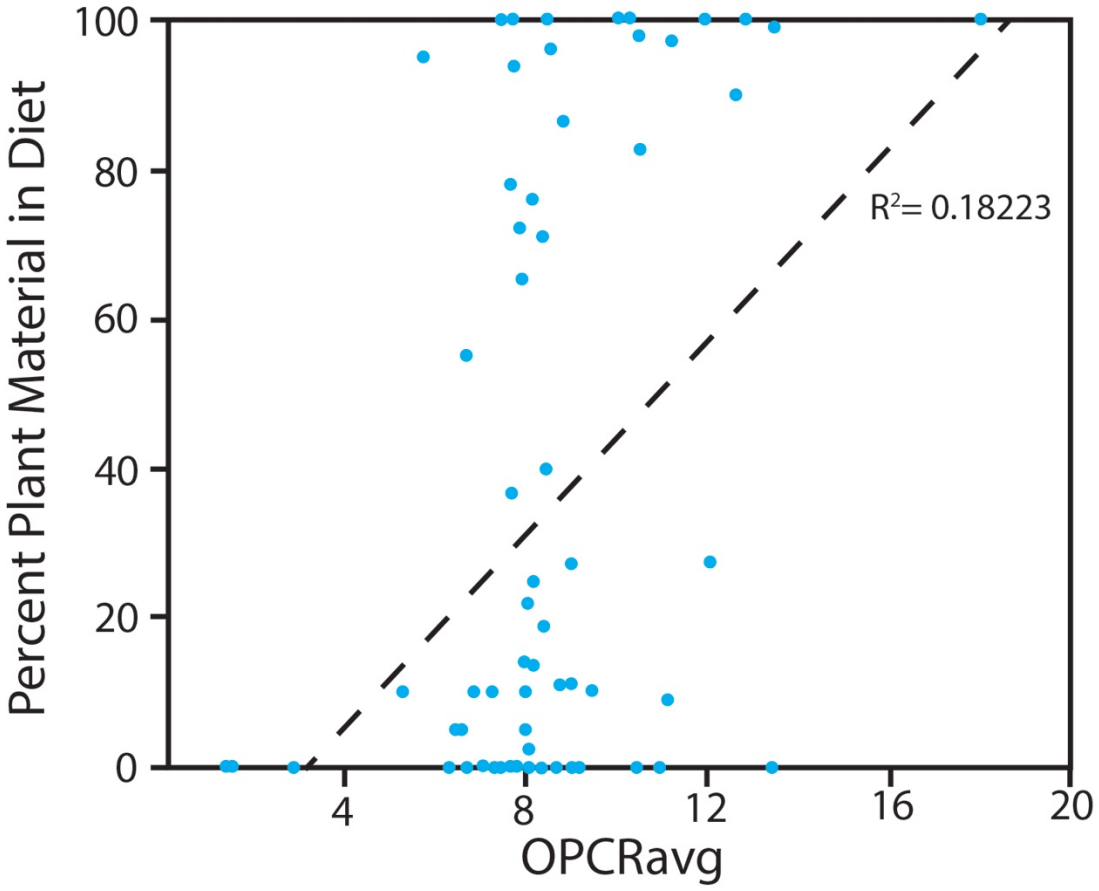


Figure S.2.2- Relationship between the average OPCR per tooth and the percent of plant material in the diet of the saurians in which volumetric dietary information could be found. Dotted line is the regression line. Note the very poor correlation.

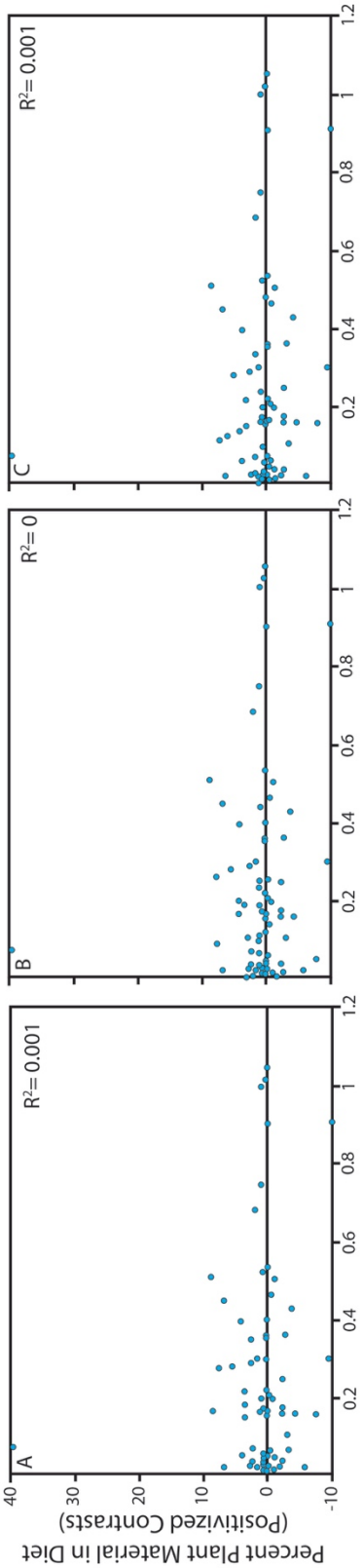


Figure S.2.3- Scatterplot results of the pIC test between the percentage of the plant material in the diet of living saurians and their OPCRavg for **(A)** Pyron et al. (2013), **(B)** Gauthier et al. (2012), and **(C)** Reeder et al. (2015) topologies. Branch lengths are derived from Hedges et al. (2015). pIC results for all three topologies display a low correlation between diet and tooth complexity.

Table S.2.1- Information on diet and element studied of each specimen investigated in this study. Abbreviations: **CAS**, California Academy of Sciences; **CBP,** Chris Bell Personal Collection; **ERP,** Eric Pianka personal collection; **FMNH**, Field Museum of Natural History; **KU,** University of Kansas; **LACM,** Los Angeles County Museum of Natural History; **MCZ,** Museum of Comparative Zoology, Harvard University; **MVZ,** Museum of Vertebrate Zoology at Berkeley; **OU,** Oklahoma University; **TMM,** Texas Memorial Museum; **SDNHM,** San Diego Natural History Museum; **UCMP,** University of California Museum of Paleontology; **UMNH,** Natural History Museum of Utah; **USNM,** National Museum of Natural History; **UT CT,** University of Texas High-Resolution X-ray Computed Tomography Facility; **YPM,** Yale Peabody Museum of Natural History. - denotes no cast number.

Name	Type	Bone Measured	Specimen Number	Cast Number
Acanthodactylus erythrurus	Bone	Left Dentary	SDNHM 65166	-
Alligator mississippiensis	UT CT	Left Dentary	TMM M-983	-
Amblyrhynchus cristatus	Cast	Left Dentary	MVZ 67721	UMNH.VP.C-287
Amblyrhynchus cristatus	Cast	Left Maxilla	UCMP 137167	UMNH.VP.C-288
Amphiglossus splendidus	UT CT	Left Dentary	FMNH 72807	-
Anolis carolinensis	UT CT	Left Dentary	FMNH 242298	-
Basiliscus basiliscus	UT CT	Left Dentary	FMNH 165622	-
Basiliscus basiliscus	Cast	Left Dentary	MVZ 79579	UMNH.VP.C-289
Basiliscus vittatus	Cast	Left Dentary	UCMP 137748	UMNH.VP.C-290
Basiliscus plumifrons	Bone	Left Dentary	MCZ R-19487	-
Bipes canaliculatus	UT CT	Left Dentary	CAS 134753	-
Brachylophus fasciatus	UT CT	Left Dentary	FMNH 210158	-
Brachylophus vitiensis	Bone	Right Dentary	MCZ R-160255	-
Caiman crocodilus	UT CT	Left Dentary	FMNH 73711	-
Callopistes maculatus	UT CT	Left Dentary	FMNH 53726	-
Calotes mystaceus	Cast	Left Dentary	CAS 243761	UMNH.VP.C-292
Chalarodon madagascariensis	UT CT	Left Dentary	YPM 12866	-
Chamaeleo senegalensis	UT CT	Left Dentary	FMNH 47572	-
Chamaeleo zeylanicus	Cast	Left Dentary	CAS Uncatalogued	UMNH.VP.C-293

Table S.2.1- Continued

Name	Type	Bone Measured	Specimen Number	Cast Number
Cnemidophorus murinus	Bone	Left Dentary	OU 39632	-
Coleonyx variegatus	UT CT	Left Dentary	YPM 14383	-
Colobosaura modesta	UT CT	Left Dentary	USNM 341978	-
Coluber constrictor	UT CT	Left Dentary	FMNH 135284	-
Conolophus subcristatus	Cast	Right Dentary	UCMP 68040	UMNH.VP.C-294
Conolophus subcristatus	Cast	Right Maxilla	UCMP 68040	UMNH.VP.C-295
Corytophanes percarinatus	Cast	Left Dentary	UCMP 123057	UMNH.VP.C-296
Crocodylus moreletii	UT CT	Left Dentary	TMM M-4980	-
Crotaphytus bicinctores	Cast	Left Dentary	CAS 200859	UMNH.VP.C-297
Crotaphytus collaris	Cast	Left Dentary	UCMP 14114	UMNH.VP.C-299
Ctenosaura pectinata	UT CT	Left Dentary	CBP Uncatalogued	-
Ctenosaura hemilopha	Cast	Left Dentary	CAS 46399	UMNH.VP.C-300
Cyclura carinata	Cast	Left Dentary	UCMP 68040	UMNH.VP.C-301
Cyclura pinguis	Bone	Right Dentary	KU 272292	-
Dicrodon guttulatum	Cast	Left Dentary	MVZ 85400	UMNH.VP.C-302
Diporiphora winneckei	Bone	Left Dentary	MCZ R-35222	-
Dipsosaurus dorsalis	UT CT	Left Dentary	YPM 14376	-
Dracaena guianensis	Cast	Left Dentary	MVZ 79247	UMNH.VP.C-303
Egernia striolata	UT CT	Left Dentary	YPM 12865	-
Egernia stokesii	Bone	Left Dentary	MCZ R-33105	-
Elgaria coerulea	Cast	Left Dentary	CAS 216644	UMNH.VP.C-304
Gambelia sila	Cast	Left Dentary	CAS 141318	UMNH.VP.C-305
Gavialis gangeticus	UT CT	Left Dentary	TMM M-5490	-
Gerrhosaurus major	Cast	Left Dentary	UCMP 137878	UMNH.VP.C-306
Gerrhosaurus major	UT CT	Left Dentary	CAS 204767	-

Table S.2.1- Continued

Name	Type	Bone Measured	Specimen Number	Cast Number
Gerrhosaurus skoogi	Bone	Left Dentary	MCZ R-50973	-
Gerrhosaurus validus	UT CT	Left Dentary	CAS 206978	-
Heloderma suspectum	Cast	Left Dentary	CAS 159492	UMNH.VP.C-307
Hemitheconyx caudicinctus	Cast	Left Dentary	CAS Uncatalogued	UMNH.VP.C-307
Iguana iguana	Bone	Left Dentary	UMNH 8084	-
Iguana iguana	Cast	Left Dentary	UCMP 123051	UMNH.VP.C-309
Intellagama lesueurii	Cast	Left Dentary	MVZ 95968	UMNH.VP.C-313
Kentropyx pelviceps	Cast	Left Dentary	MVZ 77092	UMNH.VP.C-310
Lacerta viridis	UT CT	Left Dentary	YPM 12858	-
Laemanctus longipes	Cast	Left Dentary	UCMP 129880	UMNH.VP.C-311
Leiocephalus barahonensis	UT CT	Left Dentary	USNM 260564	-
Leiocephalus inaguae	Bone	Left Dentary	MCZ R-154263	-
Leiolepis belliana	UT CT	Left Dentary	USNM 205722	-
Microlophus peruvianus	Cast	Left Dentary	UCMP 141136	UMNH.VP.C-319
Moloch horridus	UT CT	Left Dentary	ERP 26638	-
Osteolaemus tetraspis	UT CT	Left Dentary	FMNH 98936	-
Paleosuchus trigonatus	Loan	Left Dentary	USNM 300660	-
Phrynosoma hernandesi	UT CT	Left Dentary	TNHC 11839	-
Phymaturus palluma	Cast	Left Dentary	MVZ 137647	UMNH.VP.C-312
Platysaurus guttatus	Bone	Left Dentary	MCZ R-44415	-
Plica umbra	Cast	Left Dentary	CAS 93242	UMNH.VP.C-314
Sauromalus ater	Cast	Left Dentary	MVZ 100404	UMNH.VP.C-315
Sauromalus obesus	Cast	Left Dentary	UCMP 137811	UMNH.VP.C-316
Sceloporus magister	Cast	Left Dentary	CAS 200862	UMNH.VP.C-317
Sceloporus variabilis	UT CT	Left Dentary	FMNH 122866	-

Table S.2.1- Continued

Name	Type	Bone Measured	Specimen Number	Cast Number
Sphenodon punctatus	UT CT	Left Dentary	YPM 9194	-
Teius teyou	Cast	Left Dentary	MVZ 92993	UMNH.VP.C-318
Tiliqua rugosa	Bone	Left Dentary	MCZ R-24456	-
Tupinambis rufescens	Cast	Left Dentary	MVZ 92987	UMNH.VP.C-320
Tupinambis teguixin	UT CT	Left Dentary	FMNH 22416	-
Uma scoparia	Cast	Left Dentary	CAS 42076	UMNH.VP.C-321
Uromastyx aegyptia	UT CT	Left Dentary	FMNH 78661	-
Uromastyx sp.	Cast	Left Dentary	UCMP 118912	UMNH.VP.C-322
Varanus niloticus	Cast	Left Dentary	MVZ 68534	UMNH.VP.C-323
Varanus olivaceus	Bone	Left Dentary	USNM 27776	-
Varanus rudicollis	Cast	Left Dentary	UCMP 137816	UMNH.VP.C-324
Varanus salvator	UT CT	Left Dentary	FMNH 35144	-
Varanus varius	Cast	Left Dentary	MVZ 77092	UMNH.VP.C-325
Xantusia riversiana	UT CT	Left Dentary	LACM 108770	-
Xenosaurus grandis	UT CT	Left Dentary	FMNH 123702	-

Table S.2.2- The total number of patches recorded for each jaw (OPCRt) at 25, 40, and 50 data rows per tooth (RPT). – indicates the patch count was not available because the program, Surfer Manipulator, crashed. See Table S.2.1 for abbreviations.

Name	Specimen Number	OPCRt at 25 RPT	OPCRt at 40 RPT	OPCRt at 50 RPT
Acanthodactylus erythrurus	SDNHM 65166	149.500	208.625	239.250
Alligator mississippiensis	TMM M-983	88.875	107.625	117.375
Amblyrhynchus cristatus	MVZ 67721	342.625	509.125	606.500
Amblyrhynchus cristatus	UCMP 137167	167.375	230.125	262.250
Amphiglossus splendidus	FMNH 72807	128.750	177.000	192.000
Anolis carolinensis	FMNH 242298	151.875	213.750	243.500
Basiliscus basiliscus	FMNH 165622	274.750	–	–
Basiliscus basiliscus	MVZ 79579	137.750	202.625	234.625
Basiliscus vittatus	UCMP 137748	244.750	331.500	379.875
Basiliscus plumifrons	MCZ R-19487	300.375	384.625	–
Bipes canaliculatus	CAS 134753	49.625	53.375	56.375
Brachylophus fasciatus	FMNH 210158	184.375	227.625	–
Brachylophus vitiensis	MCZ R-160255	84.375	138.250	153.000
Caiman crocodilus	FMNH 73711	115.750	148.500	194.250
Callopistes maculatus	FMNH 53726	100.250	107.375	110.250
Calotes mystaceus	CAS 243761	241.375	215.625	237.250
Chalarodon madagascariensis	YPM 12866	206.500	236.750	–
Chamaeleo senegalensis	FMNH 47572	112.750	141.000	158.875
Chamaeleo zeylanicus	CAS Uncatalogued	135.750	167.875	179.625
Cnemidophorus murinus	OU 39632	64.875	66.625	68.125
Coleonyx variegatus	YPM 14383	243.125	346.375	411.375
Colobosaura modesta	USNM 341978	195.000	223.125	245.000
Coluber constrictor	FMNH 135284	75.375	85.750	92.000
Conolophus subcristatus	UCMP 68040	177.875	304.750	369.250
Conolophus subcristatus	UCMP 68040	150.375	271.875	346.125
Corytophanes percarinatus	UCMP 123057	123.250	188.000	213.375
Crocodylus moreletii	TMM M-4980	78.375	103.875	122.125
Crotaphytus bicinctores	CAS 200859	190.375	222.250	236.125
Crotaphytus collaris	UCMP 14114	111.250	156.375	182.750
Ctenosaura pectinata	CBP Uncatalogued	155.625	201.875	232.375
Ctenosaura hemilopha	CAS 46399	114.000	177.000	213.250
Cyclura carinata	UCMP 68040	91.125	143.500	177.500
Cyclura pinguis	KU 272292	182.875	292.375	357.250
Dicrodon guttulatum	MVZ 85400	201.875	259.250	293.000
Diporiphora winneckei	MCZ R-35222	89.500	100.000	101.500

Table S.2.2- Continued

Name	Specimen Number	OPCRt at 25 RPT	OPCRt at 40 RPT	OPCRt at 50 RPT
Dipsosaurus dorsalis	YPM 14376	235.000	281.750	–
Dracaena guianensis	MVZ 79247	80.375	120.625	161.250
Egernia striolata	YPM 12865	160.125	202.875	232.000
Egernia stokesii	MCZ R-33105	179.000	206.000	232.250
Elgaria coerulea	CAS 216644	147.500	197.000	229.250
Gambelia sila	CAS 141318	159.000	205.125	235.000
Gavialis gangeticus	TMM M-5490	24.875	93.625	126.875
Gerrhosaurus major	UCMP 137878	148.500	213.500	254.375
Gerrhosaurus major	CAS 204767	179.750	233.250	267.250
Gerrhosaurus skoogi	MCZ R-50973	157.250	210.625	242.750
Gerrhosaurus validus	CAS 206978	156.500	204.500	231.375
Heloderma suspectum	CAS 159492	6.625	25.125	33.125
Hemitheconyx caudicinctus	CAS Uncatalogued	264.500	337.000	–
Iguana iguana	UMNH 8084	156.500	219.875	258.250
Iguana iguana	UCMP 123051	220.375	326.375	386.125
Intellagama lesueurii	MVZ 95968	128.500	168.875	186.625
Kentropyx pelviceps	MVZ 77092	177.000	249.000	268.625
Lacerta viridis	YPM 12858	161.375	187.125	212.625
Laemanctus longipes	UCMP 129880	198.250	239.625	276.625
Leiocephalus barahonensis	USNM 260564	220.370	255.625	–
Leiocephalus inaguae	MCZ R-154263	162.625	188.250	207.000
Leiolepis belliana	USNM 205722	85.750	106.000	118.125
Microlophus peruvianus	UCMP 141136	174.625	198.500	222.125
Moloch horridus	ERP 26638	105.875	127.500	139.500
Osteolaemus tetraspis	FMNH 98936	83.375	102.000	110.250
Paleosuchus trigonatus	USNM 300660	151.000	170.375	176.875
Phrynosoma hernandesi	TNHC 11839	151.750	165.125	177.750
Phymaturus palluma	MVZ 137647	203.000	274.375	309.375
Platysaurus guttatus	MCZ R-44415	121.750	142.125	165.500
Plica umbra	CAS 93242	196.250	240.625	265.875
Sauromalus ater	MVZ 100404	215.625	365.625	432.500
Sauromalus obesus	UCMP 137811	256.500	326.375	360.500
Sceloporus magister	CAS 200862	239.875	288.750	–
Sceloporus variabilis	FMNH 122866	162.000	193.250	213.125
Sphenodon punctatus	YPM 9194	142.625	169.750	190.500
Teius teyou	MVZ 92993	176.000	198.375	219.250
Tiliqua rugosa	MCZ R-24456	92.000	96.125	101.500

Table S.2.2- Continued

Name	Specimen Number	OPCRt at 25 RPT	OPCRt at 40 RPT	OPCRt at 50 RPT
Tupinambis rufescens	MVZ 92987	107.125	143.625	168.625
Tupinambis teguixin	FMNH 22416	133.875	176.750	213.500
Uma scoparia	CAS 42076	162.875	176.000	189.500
Uromastyx aegyptia	FMNH 78661	118.250	138.875	145.125
Uromastyx sp.	UCMP 118912	125.500	164.000	184.125
Varanus niloticus	MVZ 68534	45.250	60.875	66.750
Varanus olivaceus	USNM 27776	59.625	69.875	74.125
Varanus rudicollis	UCMP 137816	28.375	59.250	75.250
Varanus salvator	FMNH 35144	87.875	102.375	117.875
Varanus varius	MVZ 77092	9.750	36.500	47.750
Xantusia riversiana	LACM 108770	109.000	128.000	143.000
Xenosaurus grandis	FMNH 123702	160.875	174.625	191.500

Table S.2.3- The average number of patches per tooth (OPCRavg) at 25, 40, and 50 data rows per tooth (RPT). This complexity value is calculated by dividing the total number of patches per jaw (OPCRt) by the number of teeth measured. – indicates the patch count was not available because the program, Surfer Manipulator, crashed. See Table S.2.1 for abbreviations.

Name	Specimen Number	OPCRavg at 25 RPT	OPCRavg at 40 RPT	OPCRavg at 50 RPT
Acanthodactylus erythrurus	SDNHM 65166	7.868	10.980	12.592
Alligator mississippiensis	TMM M-983	5.230	6.331	6.880
Amblyrhynchus cristatus	MVZ 67721	18.033	26.796	31.921
Amblyrhynchus cristatus	UCMP 137167	13.948	19.177	21.854
Amphiglossus splendidus	FMNH 72807	8.047	11.063	12.000
Anolis carolinensis	FMNH 242298	7.232	10.179	11.595
Basiliscus basiliscus	FMNH 165622	9.813	–	–
Basiliscus basiliscus	MVZ 79579	8.103	11.919	13.801
Basiliscus vittatus	UCMP 137748	11.125	15.068	17.267
Basiliscus plumifrons	MCZ R-19487	12.015	15.385	–
Bipes canaliculatus	CAS 134753	8.270	8.896	9.390
Brachylophus fasciatus	FMNH 210158	10.243	12.646	–
Brachylophus vitiensis	MCZ R-160255	7.670	12.568	13.909
Caiman crocodilus	FMNH 73711	6.809	8.735	10.792
Callopistes maculatus	FMNH 53726	7.710	8.260	8.480
Calotes mystaceus	CAS 243761	9.360	12.684	13.956
Chalarodon madagascariensis	YPM 12866	8.604	9.865	–
Chamaeleo senegalensis	FMNH 47572	6.260	7.833	8.830
Chamaeleo zeylanicus	CAS Uncatalogued	7.985	9.875	10.566
Cnemidophorus murinus	OU 39632	8.109	8.328	8.516
Coleonyx variegatus	YPM 14383	7.367	10.496	12.466
Colobosaura modesta	USNM 341978	7.800	8.925	9.800
Coluber constrictor	FMNH 135284	7.538	8.575	9.200
Conolophus subcristatus	UCMP 68040	10.463	17.926	21.721
Conolophus subcristatus	UCMP 68040	10.741	19.420	24.723
Corytophanes percarinatus	UCMP 123057	7.703	11.750	13.336
Crocodylus moreletii	TMM M-4980	6.531	8.656	10.177
Crotaphytus bicinctores	CAS 200859	8.653	10.102	10.733
Crotaphytus collaris	UCMP 14114	7.416	10.425	12.183
Ctenosaura pectinata	CBP Uncatalogued	7.411	9.613	11.065
Ctenosaura hemilopha	CAS 46399	8.769	13.615	16.404
Cyclura carinata	UCMP 68040	5.695	8.969	11.094

Table S.2.3- Continued

Name	Specimen Number	OPCRavg at 25 RPT	OPCRavg at 40 RPT	OPCRavg at 50 RPT
Cyclura pinguis	KU 272292	8.313	13.290	16.239
Dicrodon guttulatum	MVZ 85400	12.600	16.203	18.313
Diporiphora winneckei	MCZ R-35222	8.950	10.000	10.150
Dipsosaurus dorsalis	YPM 14376	11.190	13.417	–
Dracaena guianensis	MVZ 79247	8.931	13.403	17.917
Egernia striolata	YPM 12865	8.428	10.678	12.211
Egernia stokesii	MCZ R-33105	8.520	9.810	11.060
Elgaria coerulea	CAS 216644	7.020	9.381	10.917
Gambelia sila	CAS 141318	7.950	10.256	11.750
Gavialis gangeticus	TMM M-5490	1.309	4.928	6.678
Gerrhosaurus major	UCMP 137878	8.250	11.861	14.132
Gerrhosaurus major	CAS 204767	8.988	11.663	13.363
Gerrhosaurus skoogi	MCZ R-50973	10.480	14.042	16.180
Gerrhosaurus validus	CAS 206978	7.825	10.225	11.569
Heloderma suspectum	CAS 159492	1.325	5.025	6.625
Hemitheconyx caudicinctus	CAS Uncatalogued	8.015	10.212	–
Iguana iguana	UMNH 8084	9.206	12.934	15.191
Iguana iguana	UCMP 123051	10.017	14.835	17.551
Intellagama lesueurii	MVZ 95968	7.139	9.382	10.368
Kentropyx pelviceps	MVZ 77092	10.412	14.647	15.801
Lacerta viridis	YPM 12858	8.069	9.356	10.631
Laemanctus longipes	UCMP 129880	9.011	10.892	12.574
Leiocephalus barahonensis	USNM 260564	10.017	11.619	–
Leiocephalus inaguae	MCZ R-154263	8.130	9.413	10.350
Leiolepis belliana	USNM 205722	7.146	8.833	9.844
Microlophus peruvianus	UCMP 141136	8.731	9.925	11.106
Moloch horridus	ERP 26638	6.228	7.500	8.206
Osteolaemus tetraspis	FMNH 98936	6.413	7.846	8.481
Paleosuchus trigonatus	USNM 300660	7.190	8.113	8.423
Phrynosoma hernandesi	TNHC 11839	7.987	8.691	9.355
Phymaturus palluma	MVZ 137647	11.900	16.140	18.190
Platysaurus guttatus	MCZ R-44415	7.609	8.883	10.344
Plica umbra	CAS 93242	10.900	13.368	14.771
Sauromalus ater	MVZ 100404	13.477	22.852	27.031
Sauromalus obesus	UCMP 137811	12.825	16.319	18.025
Sceloporus magister	CAS 200862	8.880	10.694	–

Table S.2.3- Continued

Name	Specimen Number	OPCRavg at 25 RPT	OPCRavg at 40 RPT	OPCRavg at 50 RPT
Sceloporus variabilis	FMNH 122866	7.714	9.202	10.149
Sphenodon punctatus	YPM 9194	7.924	9.431	10.583
Teius teyou	MVZ 92993	11.733	13.225	14.617
Tiliqua rugosa	MCZ R-24456	7.667	8.010	8.458
Tupinambis rufescens	MVZ 92987	7.650	10.259	12.040
Tupinambis teguixin	FMNH 22416	7.875	10.397	12.559
Uma scoparia	CAS 42076	8.140	8.800	9.475
Uromastyx aegyptia	FMNH 78661	8.446	9.920	10.366
Uromastyx sp.	UCMP 118912	8.367	10.933	12.275
Varanus niloticus	MVZ 68534	5.656	7.609	8.344
Varanus olivaceus	USNM 27776	6.625	7.764	8.236
Varanus rudicollis	UCMP 137816	2.838	5.925	7.525
Varanus salvator	FMNH 35144	7.323	8.531	9.823
Varanus varius	MVZ 77092	1.390	5.214	6.800
Xantusia riversiana	LACM 108770	8.385	9.846	11.000
Xenosaurus grandis	FMNH 123702	8.044	8.731	9.575

Table S.2.4- The total number of patches per isolated tooth (OPCRit) at 25, 40, and 50 data rows per tooth (RPT). Each tooth measured was the most complex tooth in the jaw. Tooth measured is counted from the anteriormost alveolus. See Table S.2.1 for abbreviations.

Name	Specimen Number	Tooth Measured	OPCRit at 25 RPT	OPCRit at 40 RPT	OPCRit at 50 RPT
A. erythrurus	SDNHM 65166	23	9.250	10.875	12.125
A. mississippiensis	TMM M-983	14	8.000	8.625	9.125
A. cristatus	MVZ 67721	16	18.750	27.250	29.875
A. cristatus	UCMP 137167	15	15.250	26.250	35.000
A. splendidus	FMNH 72807	15	8.875	9.625	10.375
A. carolinensis	FMNH 242298	22	9.375	10.625	11.875
B. basiliscus	FMNH 165622	24	7.250	9.000	9.250
B. basiliscus	MVZ 79579	22	12.625	18.375	21.000
B.vittatus	UCMP 137748	19	10.125	15.750	16.000
B. plumifrons	MCZ R-19487	16	11.875	18.375	21.500
B. canaliculatus	CAS 134753	5	8.250	8.625	9.500
B. fasciatus	FMNH 210158	12	10.500	11.125	12.625
B. vitiensis	MCZ R-160255	14	12.875	18.125	19.750
C. crocodilus	FMNH 73711	18	8.125	8.000	8.125
C. maculatus	FMNH 53726	18	8.250	8.625	8.750
C. mystaceus	CAS 243761	16	14.250	19.875	22.25
C. madagascariensis	YPM 12866	20	8.875	9.750	10.500
C. senegalensis	FMNH 47572	16	12.750	24.625	28.875
C. zeylanicus	CAS Uncatalogued	12	10.250	14.250	15.625
C. murinus	OU 39632	13	8.250	8.500	8.500
C. variegatus	YPM 14383	39	8.250	9.000	10.625
C. modesta	USNM 341978	22	8.125	8.125	8.25
C. constrictor	FMNH 135284	8	8.250	10.000	11.000
C. subcristatus	UCMP 68040	18	7.500	21.125	28.250
C. subcristatus	UCMP 68040	13	8.250	16.500	22.125
C. percarinatus	UCMP 123057	19	11.500	15.500	16.250
C. moreletii	TMM M-4980	13	8.000	8.250	8.875
C. bicinctores	CAS 200859	25	9.000	11.250	12.625
C. collaris	UCMP 14114	14	9.375	13.125	15.000
C. pectinata	CBP Uncatalogued	27	12.250	17.250	18.125
C. hemilopha	CAS 46399	14	7.750	9.750	10.750
C. carinata	UCMP 68040	17	8.125	12.750	18.000
C. pinguis	KU 272292	22	10.125	21.750	23.750

Table S.2.4- Continued

Name	Specimen Number	Tooth Measured	OPCRit at 25 RPT	OPCRit at 40 RPT	OPCRit at 50 RPT
D. guttulatum	MVZ 85400	14	17.750	29.000	32.375
D. winneckei	MCZ R-35222	11	8.250	8.750	8.875
D. dorsalis	YPM 14376	15	10.500	12.375	13.375
D. guianensis	MVZ 79247	10	12.000	17.125	19.500
E. striolata	YPM 12865	21	8.250	9.125	9.000
E. stokesii	MCZ R-33105	19	8.000	8.125	8.500
E. coerulea	CAS 216644	23	8.875	10.875	12.875
G. sila	CAS 141318	17	14.125	16.875	17.375
G. gangeticus	TMM M-5490	23	8.125	9.625	10.625
G. major	UCMP 137878	19	10.000	14.750	18.750
G. major	CAS 204767	20	8.250	8.500	8.625
G. skoogi	MCZ R-50973	15	10.625	13.500	16.000
G. validus	CAS 206978	23	8.000	10.625	13.625
H. suspectum	CAS 159492	4	8.875	15.375	16.500
H. caudicinctus	CAS Uncatalogued	31	6.750	10.625	11.875
I. iguana	UMNH 8084	10	10.750	13.625	15.500
I. iguana	UCMP 123051	9	8.875	17.000	24.375
I. lesueurii	MVZ 95968	15	9.000	10.000	11.625
K. pelviceps	MVZ 77092	21	14.125	21.625	22.500
L. viridis	YPM 12858	24	7.625	9.500	9.750
L. longipes	UCMP 129880	22	10.625	16.25	20.375
L. barahonensis	USNM 260564	19	11.625	13.375	15.125
L. inaguae	MCZ R-154263	20	9.500	9.750	10.250
L. belliana	USNM 205722	9	11.125	11.875	12.125
M. peruvianus	UCMP 141136	18	12.625	13.125	13.500
M. horridus	ERP 26638	14	9.125	10.125	9.625
O. tetraspis	FMNH 98936	13	8.250	8.625	9.000
P. trigonatus	USNM 300660	20	8.000	8.000	9.500
P. hernandesi	TNHC 11839	20	8.000	8.125	8.250
P. palluma	MVZ 137647	16	13.375	21.750	24.000
P. guttatus	MCZ R-44415	14	8.125	8.750	9.250
P. umbra	CAS 93242	10	12.125	15.500	17.500
S. ater	MVZ 100404	15	10.750	23.750	28.750
S. obesus	UCMP 137811	21	12.625	26.250	34.625
S. magister	CAS 200862	21	8.250	9.125	10.250
S. variabilis	FMNH 122866	24	8.000	8.125	8.625

Table S.2.4- Continued

Name	Specimen Number	Tooth Measured	OPCRit at 25 RPT	OPCRit at 40 RPT	OPCRit at 50 RPT
S. punctatus	YPM 9194	18	12.000	13.875	14.625
T. teyou	MVZ 92993	14	13.750	16.75	20.375
T. rugosa	MCZ R-24456	10	8.000	8.000	8.000
T. rufescens	MVZ 92987	17	9.625	12.000	14.500
T. teguixin	FMNH 22416	18	7.500	8.500	9.250
U. scoparia	CAS 42076	21	9.000	9.500	10.250
U. aegyptia	FMNH 78661	13	8.625	10.000	12.625
U. sp.	UCMP 118912	15	8.875	10.250	11.875
V. niloticus	MVZ 68534	10	9.000	12.625	15.500
V. olivaceus	USNM 27776	10	8.125	8.750	9.250
V. rudicollis	UCMP 137816	9	6.250	13.250	17.875
V. salvator	FMNH 35144	9	8.000	8.125	8.250
V. varius	MVZ 77092	6	7.000	10.250	13.125
X. riversiana	LACM 108770	11	9.000	8.875	9.625
X. grandis	FMNH 123702	19	8.000	8.626	8.500

References

Auffenberg, W. 1988. Gray's Monitor Lizard. University of Florida Press, Gainesville, Florida, 419 pp.

Barrett, P. M. 2000. Prosauropod dinosaurs and iguanas - speculations on the diets of extinct reptiles; pp. 42–78 in H. D. Sues (ed.), Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record.

Baum, D. A. and S. D. Smith. 2013. Tree Thinking: An introduction to phylogenetic biology. Roberts and Company Publishers, Greenwood Village, Colorado, 496 pp.

Bell, C. J., J. I. Mead, and S. L. Swift. 2009. Cranial osteology of *Moloch horridus* (Reptilia: Squamata: Agamidae). Records of the Western Australian Museum 25:201–237.

Bever, G. S., T. R. Lyson, D. J. Field, and B. A. S. Bhullar. 2015. Evolutionary origin of the turtle skull. Nature 525:239–242.

Boyer, D. M., A. R. Evans, and J. Jernvall. 2010. Evidence of dietary differentiation among late Paleocene-early Eocene plesiadapids (Mammalia, primates). American Journal of Physical Anthrophology 142:194–210.

Brizuela, S., and A. M. Albino. 2009. The dentition of the Neotropical lizard genus *Teius* Merrem 1820 (Squamata Teiidae). Tropical Zoology 22:183–193.

Brochu, C. A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. Journal of Vertebrate Paleontology 19:9–100.

Brown, G. W. 1991. Ecological feeding analysis of south-eastern Australian scincids (Reptilia- Lacertilia). Australian Journal of Zoology 39:9–29.

Bunn, J. M., D. M. Boyer, Y. Lipman, E. M. St Clair, J. Jernvall, and I. Daubechies. 2011. Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination. American Journal of Physical Anthropology 145:247–261.

Cleuren, J., and F. de Vree. 2000. Feeding in crocodilians; pp. 337–358 in K. Schwenk (ed.), Feeding: form, function, and evolution in tetrapod vertebrates. Academic Press, San Diego.

Colbert, E. H. 1967. Adaptations for gliding in the lizard *Draco*. American Museum Novitates 2283:1–20.

Conant, R. 1955. Saurian shell crusher. Nature Magazine 48:85–86.

Cooper, J. S., and J. C. Poole. 1973. The dentition and dental tissues of the agamid lizard, *Uromastyx*. Journal of Zoology 169:85–100.

Cooper, J. S., J. C. Poole, and R. Lawson. 1970. The dentition of agamid lizards with special reference to tooth replacement. Journal of Zoology 162:85–98.

Cooper, W. E., and L. J. Vitt. 2002. Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology 257:487–517.

Crawford, N. G., B. C. Faircloth, J. E. McCormack, R. T. Brumfield, K. Winkler, and T. C. Glenn. 2012. More than 1000 ultraconserved elements provide evidence that turtles are the sister group of archosaurs. Biology Letters 8:783–786.

Crawford, N. G., J. F. Parham, A. B. Sellas, B. C. Faircloth, T. C. Glenn, T. J. Papenfuss, J. B. Henderson, M. H. Hansen, and W. B. Simison. 2015. A phylogenomic analysis of turtles. Molecular Phylogenetics and Evolution 83:250–257.

Dalrymple, G. H. 1979. On the Jaw Mechanism of the Snail-Crushing Lizards, *Dracaena* Daudin 1802 (Reptilia, Lacertilia, Teiidae). Journal of Herpetology 13:303–311.

Delany, M. F., and C. L. Abercrombie. 1986. American Alligator food habits in northcentral Florida. Journal of Wildlife Managment 50:348–353.

Dessem, D. 1985. Ontogenetic Changes in the Dentition and Diet of *Tupinambis* (Lacertilia: Teiidae). Copeia 1985:245–247.

Duffield, G. A., and C. M. Bull. 1998. Seasonal and ontogenetic changes in the diet of the Australian skink *Egernia stokesii*. Herpetologica 54:414–419.

Durtsche, R. D. 2000. Ontogenetic plasticity of food habitats in the Mexican spiny-tailed iguana, *Ctenosaura pectinata*. Oecologia 124:185–195.

Edmund, A. G. 1969. Dentition; pp. 117–200 in C. Gans, d'A. Bellairs, and T. Parsons (eds.), Biology of the Reptilia, pt. 1. Academic Press, New York and London.

Erickson, G. M., P. M. Gignac, S. J. Steppan, A. K. Lappin, K. A. Vliet, J. D. Brueggen, B. D. Inouye, D. Kledzik, and G. J. Webb. 2012. Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. PLoS One 7:e31781.

Espinoza, R. E., J. J. Wiens, and C. R. Tracy. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. Proceedings of the National Academy of Sciences USA 101:16819–16824.

Estes, R., and E. E. Williams. 1984. Ontogenetic Variation in the Molariform Teeth of

Lizards. Journal of Vertebrate Paleontology 4:96–107.

Evans, A. R. 2013. Shape descriptors as ecometrics in dental ecology. Hystrix, the Italian Journal of Mammalogy 24:133–140.

Evans, A. R., and C. M. Janis. 2014. The evolution of high dental complexity in the horse lineage. Annales Zoologici Fennici 51:73–79.

Evans, A. R., and G. D. Sanson. 1998. The effect of tooth shape on the breakdown of insects. Journal of Zoology 246:391–400.

Evans, A. R., G. P. Wilson, M. Fortelius, and J. Jernvall. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

Field, D. J., J. A. Gauthier, B. L. King, D. Pisani, T. R. Lyson, and K. J. Peterson. 2014. Towards consilience in reptile phylogeny: miRNAs support an archosaur, not lepidosaur, affinity for turtles. Evolution and Development 16:189–196.

Foley, W. J., A. Bouskila, A. Shkolnik, and I. Choshniak. 1992. Microbial digestion in the herbivorous lizard *Uromastyx aegyptius* (Agamidae). Journal of Zoology 226:387–398.

Freeman, P. W. 1979. Specialized Insectivory: Beetle-Eating and Moth-Eating Molossid Bats. Journal of Mammalogy 60:467–479.

Furness, R. W. 1988a. The predation of Tern chicks by sheep. Bird Study 35:199–202.

Furness, R. W. 1988b. Predation on ground-nesting seabirds by island populations of red deer *Cervus elaphus* and sheep *Orvis*. Journal of Zoology 216:565–573.

Galton, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs; pp. 203–221 in K. Padian (ed.), The Beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary. Cambridge University Press, Cambridge, UK.

Gauthier, J. A., A. G. Kluge, and T. Rowe. 1988. The early evolution of the Amniota; pp. 103–155 in: M. J. Benton (ed.), The Phylogeny and classification of the tetrapods, 1: Amphibians, Reptiles, Birds. Clarendon Press, Oxford, UK.

Gauthier, J. A., M. Kearney, J. A. Maisano, O. Rieppel, and A. D. B. Behlke. 2012. Assembling the Squamate Tree of Life: Perspectives from the Phenotype and the Fossil Record. Bulletin of the Peabody Museum of Natural History 53:3–308.

Godfrey, L. R., J. M. Winchester, S. J. King, D. M. Boyer, and J. Jernvall. 2012. Dental topography indicates ecological contraction of lemur communities. American Journal of Physical Anthropology 148:215–227.

Greene, H. W. 1982. Dietary and phenotypic diversity in lizards - why are some organisms specialized?; pp. 107–128 in D. Mossakowski, and G. Roth (eds.), Environmental adaptation and evolution. Gustav Fischer, New York.

Greer, A. 1976. On the evolution of the giant Cape Verde scincid lizard *Macroscincus coctei*. Journal of Natural History 10:691–712.

Hammer, O., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9.

Hedges, S. B., J. Marin, M. Suleski, M. Paymer, and S. Kumar. 2015. Tree of life reveals clock-like speciation and diversification. Molecular Biology and Evolution 32:835–845.

Herrel, A., K. Huyghe, B. Vanhooydonck, T. Backeljau, K. Breugelmans, I. Grbac, R. Van Damme, and D. J. Irschick. 2008. Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. Proceedings of the National Academy of Sciences USA 105:4792–4795.

Herrel, A., B. Vanhooydonck, and R. Van Damme. 2004. Omnivory in lacertid lizards: adaptive evolution or constraint? Journal of Evolutionary Biology 17:974–984.

Hirth, H. F. 1963. The ecology of two lizards on a tropical beach. Ecological Monographs 33:83–112.

Hollenshead, M. G., J. I. Mead, and S. L. Swift. 2011. Late Pleistocene *Egernia* group skinks (Squamata: Scincidae) from Devils Lair, Western Australia. Alcheringa 35:31–51.

Hotton, N. 1955. A Survey of Adaptive Relationships of Dentition to Diet in the North American Iguanidae. American Midland Naturalist 53:88–114.

Hutchinson, M. N. 1989. A Skeletal Specimen of the Giant Skink Macroscincus coctei in the American Musuem of Natural History. Copeia 1989:492–494.

Iverson, J. B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum: Biological Sciences 24:175–358.

Iverson, J. B. 1980. Colic modifications in iguanine lizards. Journal of Morphology 163:79–93.

Jaksić, F. M., and K. Schwenk. 1983. Natural History Observations on *Liolaemus magellanicus*, the Southernmost Lizard in the World. Herpetologica 39:457–461.

Jones, M. E. H. 2009. Dentary tooth shape in *Sphenodon* and its fossil relatives (Diapsid:

Lepidosauria: Rhynchocephalia). Frontiers of Oral Biology 13:9–15.

King, G. 1996. Reptiles and Herbivory. 157 pp. Chapman & Hall, London.

Kley, N. J., J. J. W. Sertich, A. H. Turner, D. W. Krause, P. M. O'Connor, and J. A. Georgi. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 30:13–98.

Lamb, T., A. M. Meeker, A. M. Bauer, and W. R. Branch. 2003. On the systematic status of the desert plated lizard (*Angolosaurus skoogi*): phylogenetic inference from DNA sequence analysis of the African Gerrhosauridae. Biological Journal of the Linnean Society 78:253–261.

Laverty, T. M., and A. P. Dobson. 2013. Dietary Overlap Between Black Caimans and Spectacled Caimans in the Peruvian Amazon. Herpetologica 69:91-101.

Loftin H. and E. L. Tyson. 1965. Iguanas as carrion eaters. Copeia 1965:515

Lönnberg, E. 1903. On the adaptations to a molluscivorous diet in *Varanus niloticus*. Arkiv fur Zoologi 1:65–83.

Losos, J. B., and H. W. Greene. 1988. Ecological and evolutionary implications of diet in monitor lizards. Biological Journal of the Linnean Society 35:379–407.

Lyson, T. R., E. A. Sperling, A. M. Heimberg, J. A. Gauthier, B. L. King, and K. J. Peterson. 2012. MicroRNAs support a turtle + lizard clade. Biology Letters 8:104–107.

Maddison, W. P., and D. R. Maddison. 2006. Mesquite: A modular system for evolutionary analysis. Version 1.1.

Magnusson, W. E., E. V. da Silva, and A. P. Lima. 1987. Diets of Amazonian Crocodilians. Journal of Herpetology 21:85–95.

Mateo, J. A., and L. F. López-Jurado. 1992. Study of dentition in lizards from Gran Canaria Island (Canary Islands) and its ecological and evolutionary significance. Biological Journal of the Linnean Society 46:39–48.

McGuire, J. A. 1996. Phylogenetic systematics of crotaphytid lizards (Reptilia: Iguania: Crotaphytidae). Bulletin of the Carnegie Museum of Natural History 32:1–143.

McNease, L., and T. Joanen. 1977. Alligator diets in relation to marsh salinity. Proceedings, Annual Conference, Southeast Association of Fish and Wildlife Agencies 31:36–40.

Metzger, K. A., and A. Herrel. 2005. Correlations between lizard cranial shape and diet: a quantitative, phylogenetically informed analysis. Biological Journal of the Linnean Society 86:433–466.

Midford, P. E., T. Garland Jr., and W. P. Maddison. 2005. PDAP Package of Mesquite.

Montanucci, R. R. 1968. Comparative dentition in four iguanid lizards. Herpetologica 24:305–315.

Nagy, K. A. 1973. Behavior, diet and reproduction in a desert lizard, *Sauromalus obesus*. Copeia 1973:93–102.

Nagy, K. A., and V. H. Shoemaker. 1984. Field energetics and food consumption of the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiological Zoology 57:281–290.

Nance, H. A. 2007. Cranial osteology of the African gerrhosaurid *Angolosaurus skoogi* (Squamata: Gerrhosauridae). African Journal of Herpetology 56:39–75.

Norell, M. A., J. M. Clark, and J. H. Hutchinson. 1994. The Late Cretaceous Alligatoroid *Brachychampsa montana* (Crocodylia): New Material and Putative Relationships. American Museum Novitates 3116:1–26.

Nydam, R. L. 1999. Polyglyphanodontinae (Squamata: Teiidae) from the medial and Late Cretaceous: new records from Utah, U.S.A. and Baja California del Norte, Mexico; pp. 303–317 in: D. D. Gillette (ed.), Vertebrate Paleontology in Utah. Utah Geological Survey, Salt Lake City, Utah.

Nydam, R. L., and R. L. Cefelli. 2005. New data on the dentition of the scincomorphan lizard *Polyglyphanodon sternbergi*. Acta Palaeontologica Polonica 50:73–78.

Ősi, A. 2013. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. Historical Biology 26:279–414.

Pauwels, O. S. G., B. Barr, M. L. Sanchez, and M. Burger. 2007. Diet records for the dwarf Crocodile, *Osteolaemus tetraspis tetraspis* in Rabi oil fields and Loango National Park, southwestern Gabon. Hamadryad 31:258–264.

Pauwels, O. S. G., V. Mamonekene, P. Dumont, W. R. Branch, M. Burger, and S. Lavoué. 2003. Diet records for *Crocodylus cataphractus* (Reptilia - Crocodylidae) at Lake Divangui Ogooue-Maratime Province, southwestern Gabon. Hamadryad 27:200–204.

Pietruszka, R. D., S. A. Hanrahan, D. Mitchell, and M. K. Seely. 1986. Lizard herbivory in a sand dune environment: the diet of *Angolosaurus skoogi*. Oecologia 70:587–591.

Pough, F. H. 1973. Lizard energetics and diet. Ecology 54:837–844.

Presch, W. 1974. A Survey of the Dentition of the Macroteiid Lizards (Teiidae: Lacertilia). Herpetologica 30:344–349.

Pyron, R. A., F. T. Burbrink, and J. J. Weins. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evolutionary Biology 13:93.

Reeder, T. W., T. M. Townsend, D. G. Mulcahy, B. P. Noonan, P. L. Wood, Jr., J. W. Sites, Jr., and J. J. Wiens. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PLoS One 10:e0118199.

Reilly, S. M., L. B. McBrayer, and D. B Miles (eds.). 2007. Lizard Ecology: The evolutionary consequences of foraging mode. Cambridge University Press, Cambridge, UK, 558 pp.

Reisz, R. R., and H. D. Sues. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates; pp. 9–41 in H. D. Sues (ed.), Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record. Cambridge University Press, Cambridge, UK.

Rieppel, O., and L. Labhardt. 1979. Mandibular Mechanics in *Varanus niloticus* (Reptilia: Lacertilia). Herpetologica 35:158–163.

Robinson, P. L. 1976. How *Sphenodon* and *Uromastyx* grow their teeth and use them; pp. 43–64 in A. A. Bellairs, and C. B. Cox (eds.), Morphology and Biology of the Reptiles. Academic Press, London, UK.

Rocha, C. F. D. 1998. Ontogenetic shift on the rate of plant consumption in a tropical lizard. Journal of Herpetology 32:274–279.

Saalfeld, D. T., W. C. Conway, and G. E. Calkins. 2011. Food Habits of American Alligators (*Alligator mississippiensis*) in East Texas. Southeastern Naturalist 10:659-672.

Santana, S. E., S. Strait, and E. R. Dumont. 2011. The better to eat you with: functional correlates of tooth structure in bats. Functional Ecology 25:839–847.

Schwenk, K. 2000. Feeding in Lepidosaurs; pp. 175–291 in K. Schwenk (ed.), Feeding: form, function and evolution in tetrapod vertebrates.

Shea, G. M. 2006. Diet of two species of bluetongue skink, *Tiliqua multifasciata* and *Tiliqua occipitalis* (Scincidae). Australian Zoologist 33:359–368.

Skinner, A., A. F. Hugall, and M. N. Hutchinson. 2011. Lygosomine phylogeny and the origins of Australian scincid lizards. Journal of Biogeography 38:1044–1058.

Smits, P. D., and A. R. Evans. 2012. Functional constraints on tooth morphology in carnivorous mammals. BMC Evolutionary Biology 12:146.

Snyder, R. C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. Copeia 1949:129–137.

Sokol, O. M. 1967. Herbivory in Lizards. Evolution 21:192–194.

Strait, S. 1993. Molar morphology and food texture among small-bodied insectivorous mammals. Journal of Mammalogy 74:391–402.

Sumida, S. S., and R. W. Murphy. 1987. Form and function of the tooth crown structure in gekkonid lizards (Reptilia, Squamata, Gekkonidae). Canadian Journal of Zoology 65:2886–2892.

Teaford, M. F., and O. J. Oyen. 1989. Live Primates and Dental Replication: New Problems and New Techniques. American Journal of Physical Anthropology 83:73–81.

Throckmorton, G. S. 1976. Oral food processing in two herbivorous lizards, *Iguana iguana* (Iguanidae) and *Uromastix aegyptius* (Agarnidae). Journal of Morphology 148:363–390.

Troyer, K. 1984a. Diet selection and digestion in *Iguana iguana*: the imporance of age and nutrient requirements. Oecologia 61:201–207.

Troyer, K. 1984b. Structureand function of the digestive tract of a herbivorous lizard *Iguana iguana*. Physiological Zoology 57:1–8.

Tucker, A. D., C. J. Limpus, H. I. McCallum, and K. R. McDonald. 1996. Ontogenetic dietary partitioning by *Crocodylus johnstoni* during the dry season. Copeia 1996:978–988.

Uetz, P. 2015. The Reptile Database.

Van Leeuwen, J. P., A. Catenazzi, and M. Holmgren. 2012. Spatial Ontogenetic and Sexual Effects on the Diet of a Teiid Lizard in Arid South America. Journal of Herpetology 45:472–477.

Van Marken Lichtenbelt, W. D. 1993. Optimal foraging of a herbivorous lizard, the green iguana in a seasonal environment. Oecologia 95:246–256.

Vervust, B., P. Pafilis, E. D. Valakos, and R. Van Damme. 2010. Anatomical and

physiological changes associated with a recent dietary shift in the lizard Podarcis sicula. Physiological and Biochemical Zoology 83:632–642.

Vidal, M. A., and J. C. Ortiz. 2003. *Callopistes palluma* (Chilean Racerunner, Iguana chilena). Cannibalism. Herpetological Review 34:364–365.

Vitt, L. J., P. A. Zani, J. P. Caldwell, and E. O. Carrillo. 1995. Ecology of the lizard *Kentropyx pelviceps* (Sauria:Teiidae) in lowland rain forest of Ecuador. Canadian Journal of Zoology 73:691–703.

Wilson, G. P., A. R. Evans, I. J. Corfe, P. D. Smits, M. Fortelius, and J. Jernvall. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460.

Wu, X.-C., D. B. Brinkman, and A. P. Russell. 1996. A new alligator from the Upper Cretaceous of Canada and the relationships of early eusuchians. Palaeontology 39:351–375.

Zahradnicek, O., M. Buchtova, H. Dosedelova, and A. S. Tucker. 2014. The development of complex tooth shape in reptiles. Frontiers in Physiology 5:74.

Zimmerman, L. C., and C. R. Tracy. 1989. Interactions between the environment and ectothermy and herbivory in reptiles. Physiological Zoology 62:374–409.

CHAPTER 3

REPEATED EVOLUTION OF HIGHLY COMPLEX DENTITIONS AND HERBIVORY IN CROCODYLIFORMS

Understanding the ecology of extinct organisms is critical for evaluating how ecosystems have evolved over time. Such inferences not only have the potential to elucidate the origins of modern ecosystems but also reveal community trophic structures not present today. In particular, analyses of feeding ecologies can document important ecological radiations and transitions over time (Wilson et al., 2012), but this can be difficult when investigating faunal assemblages with members that have distant or no extant descendants. For example, recent work on Mesozoic nonmarine ecosystems has suggested that habitats lacking diverse mammal assemblages contain crocodyliforms fulfilling ecological roles they do not occupy today (O'Connor et al., 2010; Ősi, 2013). However, without a firm understanding of these animals' dietary habits, any reconstruction of ecosystem niche structure remains speculative.

Extant crocodylians are conservative in their morphology and ecology, largely semiaquatic generalist carnivores, which contrasts with the striking morphological disparity of extinct lineages (Benton and Clark, 1988; Clark, 1994; Young et al., 2010; Ősi, 2013; Stubbs et al., 2013). Many extinct crocodyliforms, particularly Mesozoic taxa outside the crown clade, possess morphological features that suggest a wide variety of ecological roles not shared with living Crocodylia, with osteological specializations that

indicate fully marine to fully terrestrial habitats (Wu et al., 1995; Sereno and Larsson, 2009; Kley et al., 2010; O'Connor et al., 2010; Young et al., 2010; Ősi, 2013; Stubbs et al., 2013). In addition, heterodonty, the condition of possessing multiple tooth morphologies within a single dentition, evolved independently multiple times in Crocodyliformes (Clark et al., 1989; Wu et al., 1995; Ősi and Weishampel, 2009; Sereno and Larsson, 2009; Kley et al., 2010; O'Connor et al., 2010; Ősi, 2013). These complex dentitions have led many workers to suggest these extinct crocodyliforms had a much wider dietary breadth than extant Crocodylia (Fig. 3.1), and that some taxa approached a mammal-like condition (i.e., heterodont dentition and/or a high degree of occlusion; Clark et al., 1989; Wu et al., 1995; O'Connor et al., 2010), but what ecological role these animals played remains unclear. Interpretations of extinct crocodyliform feeding ecologies have ranged from carnivores (Ősi, 2013), to insectivores (Gomani, 1997), omnivores (Marinho and Carvalho, 2009; Soto et al., 2011), and herbivores (Wu et al., 1995; Buckley et al., 2000; Fiorelli and Calvo, 2008; Sereno and Larsson, 2009; Kley et al., 2010). Many extinct heterodont crocodyliforms are outside the crown and possess tooth morphologies that have no modern analog, which severely weakens dietary inferences based solely on comparative studies using modern crocodylians (Ősi, 2013).

To infer the diet of extinct crocodyliforms with distinctive heterodont dentitions, I obtained μCT and CT scans of the dentitions from 14 different taxa to quantify dental complexity using a geographic information systems (GIS) analysis called orientation patch count rotated (OPCR; Evans et al., 2007; Wilson et al., 2012). OPCR is a quantitative method that measures dental complexity by converting dentitions into digital elevation models and grouping contiguous pixels with a similar orientation (based on

their cardinal and ordinal directions) together into patches (Fig. 3.1). This analysis does not require morphological homologies to be established, as it examines the topographic complexity of the entire tooth row (Evans et al., 2007).

Previous studies have demonstrated phenotypic tooth complexity correlates with diet in extant and extinct mammals (Evans et al., 2007; Santana et al., 2011; Smits and Evans, 2012; Wilson et al., 2012; Evans and Janis, 2014) and extant dentigerous saurians (Chapter 1); thus, this method has broad applicability for amniote dentitions and is appropriate to use with crocodyliforms. In extant saurians (excluding edentulous birds and turtles) and mammals, OPCR values for the dentition increase with the relative amount of plant matter consumed, with herbivores typically possessing more complex dentitions than carnivores (Fig. 3.2; Evans et al., 2007; Santana et al., 2011; Chapter 2). In extant saurians, both the OPCR of the most complex tooth as well as the average OPCR value (i.e., total OPCR for the tooth row divided by number of teeth) correlate with diet (Chapter 2). This dataset included six extant crocodylian species from all major lineages.

To infer dietary categories for the extinct crocodyliforms sampled, I calculated OPCR values for tooth rows and individual teeth; these results were then compared with the range of values across dietary categories (carnivore, durophage, insectivore, omnivore, and herbivore) observed for the same measurements in extant dentigerous saurians (Fig. 3.2; Chapter 2; see Supplementary Information for more details on methods). Sampled extinct crocodyliform taxa included three crown crocodylians (*Boverisuchus*, *Brachychampsa*, and "*Allognathosuchus*"; Figs. S.3.1–3), two early eusuchians (*Acynodon* and *Iharkutosuchus*; Figs. S.3.4–5), six notosuchians

(*Candidodon*, *Simosuchus, Chimaerasuchus*, *Pakasuchus*, *Mariliasuchus*, and *Armadillosuchus*; Figs. S.3.6–11), and three early crocodyliforms (*Edentosuchus* and two unnamed taxa from the Lower Jurassic Kayenta Formation; Figs. S.3.12–14).

The Eocene crocodylian *Boverisuchus vorax* possesses the simplest dentition: it has labiolingually compressed serrated "ziphodont" teeth similar to theropod dinosaurs, many varanid lizards, and sebecosuchian crocodyliforms (Figs. 3.1–2; D'Amore and Blumenschine, 2009; Larson and Evans, 2015). The mean OPCR and the OPCR value of the most complex tooth (7.042 patches per tooth [PPT] and 7.875 PPT, respectively) overlaps with the values for extant crocodylians which, when combined with its morphology, strongly suggests a carnivorous diet (Fig. 3.2). The notosuchian crocodyliforms *Mariliasuchus amarali*, *Armadillosuchus arrudai*, and *Candidodon itapecuruense* have intermediate individual tooth (8.75, 9.75, 11.375 PPT, respectively) and mean OPCR (7.77, 9.44, and 7.77 PPT, respectively) complexities that make dietary reconstructions more uncertain (Fig. 3.2). These values fall in the range of both insectivorous and omnivorous extant saurians, and these crocodyliform taxa do not possess additional discrete dental character states that would allow placement in one of these two dietary categories (cf. Chapter 2). *Armadillosuchus* had a snout-vent length over 650 mm (Marinho and Carvalho, 2009), which places it outside the body size range (≤ 300 mm) of extant saurian insectivores (Chapter 2), suggesting an omnivorous diet is more likely for this taxon (Fig. 3.2).

Simosuchus clarki possesses a multicusp, heterodont dentition similar to extant herbivorous iguanids (e.g., *Amblyrhynchus cristatus* and *Ctenosaura hemilopha*; Kley et al., 2010), but it is not recovered as an unambiguous herbivore based solely on its

individual tooth complexity value (Fig. 3.2A). When all teeth preserved in the left dentary are analyzed, *Simosuchus* is clearly recovered as an herbivore (Fig. 3.2B), although this too is likely an underestimate of dental complexity. The teeth measured, from the mesial part of the dentition, are the simplest found in the dentary; such teeth only possess three cusps whereas more distally positioned teeth of this taxon may possess upwards of seven cusps (Kley at al., 2010). Therefore, my OPCR results underestimate the average complexity for this taxon, and I agree with Kley et al. (2010) in inferring that *Simosuchus* was an herbivore.

Acynodon iberoccitanus, "*Allognathosuchus*", *Chimaerasuchus paradoxus*, *Edentosuchus tienshanensis*, two undescribed *Edentosuchus*-like taxa from the Kayenta Formation (UCMP 130082 and UCMP 97638), *Iharkutosuchus makadii*, and *Pakasuchus kapilimai* possess dentitions with complexity values that are equal to or greater than those of extant saurian herbivores (single tooth OPCR > 14.25 PPT and average OPCR > 10 PPT; Fig. 3.2). Of these, "*Allognathosuchus*" is likely a durophage, given the similarity of its tooth morphology to extant reptilian durophages (Chapter 1), and the fact that its most complex tooth is highly worn and therefore its complexity is overestimated. This is apparent when comparing average OPCR values, where "*Allognathosuchus*" has lower complexity values similar to the Cretaceous alligatoroid *Brachychampsa*, which is also inferred to be a durophage (Fig. 3.2B). *Pakasuchus*, a small-bodied notosuchian that is characterized by extreme variation in dental morphology and mammal-like levels of occlusion (O'Connor et al., 2010), is reconstructed as a probable herbivore. This taxon possesses a unique combination of enlarged mesially placed caniniform teeth, simple, conically shaped premolariform teeth, and complex, distally placed molariform teeth

(O'Connor et al., 2010). Although the average OPCR value (Fig. 3.2B) for this taxon overlaps with those of omnivores, the most complex tooth is within the range of values observed only in herbivores (Fig. 3.2A). The remaining taxa (*Acynodon*, *Chimaerasuchus*, *Edentosuchus*, UCMP 130082, UCMP 97638, and *Iharkutosuchus*) are unambiguous herbivores; among these, UCMP 130082, *Chimaerasuchus*, and *Iharkutosuchus* possess isolated tooth complexity values greater than any measured extant saurian (Fig. 3.2A). Although *Iharkutosuchus* and *Acynodon* possess labiolingually expanded distal teeth similar to "*Allognathosuchus*" and *Brachychampsa*, their dentitions are characterized by subtle cusps or distinct grooves – features that are not observed in extant durophagous saurians (e.g., *Dracaena guianensis*).

Although previous workers have suggested that herbivory evolved separately in one or more different lineages of Mesozoic crocodyliforms (Wu et al., 1995; Buckley et al., 2000; Fiorelli and Calvo, 2008; Sereno and Larsson, 2009; Kley et al., 2010), my data demonstrate that the occurrence of herbivory in these taxa is more common than previously thought. The OPCR results suggest that herbivory independently evolved a minimum of three times among Crocodyliformes: once in *Edentosuchus*-like early crocodyliforms, at least once and possibly three times in Notosuchia, and once in Hylaeochampsidae (Fig. 3.3). Within Notosuchia, the number of inferred origins of herbivory may change as future taxon sampling is increased. With that caveat, at least three origins of herbivory with Notosuchia is not unreasonable given that many of the intervening unsampled taxa (e.g., uruguaysuchids, peirosaurids, *Notosuchus*, *Caipirasuchus*, and sebecosuchians) do not have dentitions that are as complex as the inferred herbivorous notosuchians (*Simosuchus*, *Pakasuchus*, and *Chimaerasuchus*)

sampled in this study.

Saurians (including crocodyliforms) are typically thought of as having less complex dentitions than synapsids (including mammals). When measured at or near the same resolution as extant mammals (50 data rows per tooth; Evans et al., 2007; Smits and Evans, 2012; Winchester et al., 2014), many crocodyliform taxa in this study (e.g., UCMP 130082, *Chimaerasuchus*, *Iharkutosuchus*) rival the dental complexities observed in living herbivorous rodents and carnivorans (Evans et al., 2007; Supplementary Table 1). Crocodyliforms independently developed unique dental forms to achieve extremely high complexities, likely for the purpose of breaking down and consuming tough-to-digest plant matter. These morphologies range from labiolingually expanded teeth with three rows of 5–7 tall cusps in *Chimaerasuchus* (Fig. 3.1D) to labiolingually expanded teeth with a central cusp or set of cusps surrounded by low secondary cusps in *Iharkutosuchus* and UCMP 130082 (Fig. 3.1E; Ősi, 2013). Similar to multituberculates (Wilson et al., 2012) and extant lizards (Chapter 2), increased dental complexity is primarily driven by increases in cusp number and relative size of the distal portion of the dentition. However, with the exception of the multicusped labiolingually compressed tooth morphology of *Simosuchus*, which is similar to extant herbivorous lizards (Hotton, 1955; Barrett, 2000; Kley et al., 2010), most herbivorous crocodyliforms developed complex molariform teeth. For example, *Pakasuchus* possess two large cusps separated by a wide, deep trough, suggesting a high level of occlusion (O'Connor et al., 2010). *Chimaerasuchus* increased dental complexity by labiolingually expanding its teeth and adding numerous tall cusps, a morphology similar to tritylodontid synapsids (e.g., Wu and Sues; 1996; Ősi, 2013). In contrast, *Acynodon* added complexity in the distal part of

the dentition through ridges and grooves. Even among closely related taxa different morphologies are present; whereas UCMP 97638 possesses bulbous distal teeth characterized by two large cusps (Sues et al., 1994: fig. 16.3), UCMP 130082 possesses labiolingually expanded teeth with a variable number of low secondary cusps around larger central cusps (Fig. 3.1E).

Previous studies have suggested that crocodyliform taxa with the highest degree of heterodonty are restricted to regions with either few or no mammaliaforms, and that the development of mammal-like dental morphologies may be related to this paucity of mammaliaforms (O'Connor et al., 2010; Ősi, 2013). Although *Iharkutosuchus*, *Acynodon*, *Chimaerasuchus*, and *Edentosuchus* were discovered in formations that lack mammaliaform fossils, mammaliaforms are known from both the Early to middle Cretaceous of China and latest Cretaceous of Europe (e.g., Zhou et al., 2003; Luo et al., 2007; Csiki-Sava et al., 2015; Lopatin and Averianov, 2015; Smith and Codrea, 2015). In contrast, the herbivorous *Edentosuchus*-like crocodyliforms from the Early Jurassic of western North America are preserved in the same formations as numerous synapsids, including herbivorous tritylodonts and mammaliaforms (Jenkins et al., 1983; Sues et al., 1994; Tykoski, 2005). The Gondwanan notosuchians *Pakasuchus* and *Simosuchus* also are found in assemblages that contain mammaliaforms (Krause et al., 2003; Rogers et al., 2013; Schultz et al., 2014). The synapsids that co-occur with these herbivorous crocodyliforms include both herbivores and omnivores (Kühne, 1956; Sues, 1986; Schultz et al., 2014). This suggests that Mesozoic heterodont crocodyliforms either directly competed with synapsids for plant materials or utilized different botanical resources. In either case, it is clear that crocodyliforms developed herbivory in the

presence of mammaliaforms and other closely related synapsids, in contrast to previous hypotheses (O'Connor et al., 2010; Ősi, 2013). This result implies that some Mesozoic ecosystems were characterized by at least two disparate clades of amniote primary consumers, indicating novel ecological interactions between these two clades that do not occur in today's ecosystems (Head et al., 2013). How the environment was able to support, in some cases, herbivorous megafauna (e.g., sauropods) with multiple groups of smaller herbivorous animals (e.g., mammals and crocodyliforms) remains an open question and an important avenue of future research.

This research is the first to quantitatively and robustly reconstruct the diet of extinct crocodyliforms and it clearly demonstrates that they occupied a much more diverse set of ecological roles, including terrestrial herbivores, than living members of this clade. The dental complexity values of these herbivorous crocodyliforms rival those of some extant herbivorous mammals. These data indicate that crocodyliform herbivory originated independently between three to five times, although this number may fluctuate, as other heterodont notosuchian taxa (e.g., *Malawisuchus mwakasyungutiensis*, *Adamantinasuchus navae*, *Yacarerani boliviensis*) remain untested. Many of these herbivorous crocodyliforms lived alongside herbivorous synapsids (including mammaliaforms), suggesting these organisms were not simply filling a "mammalian" ecological role (i.e., small-bodied, terrestrial herbivore). This demonstrates a fundamentally different dynamic in Mesozoic ecosystems than what is observed in modern terrestrial ecosystems.

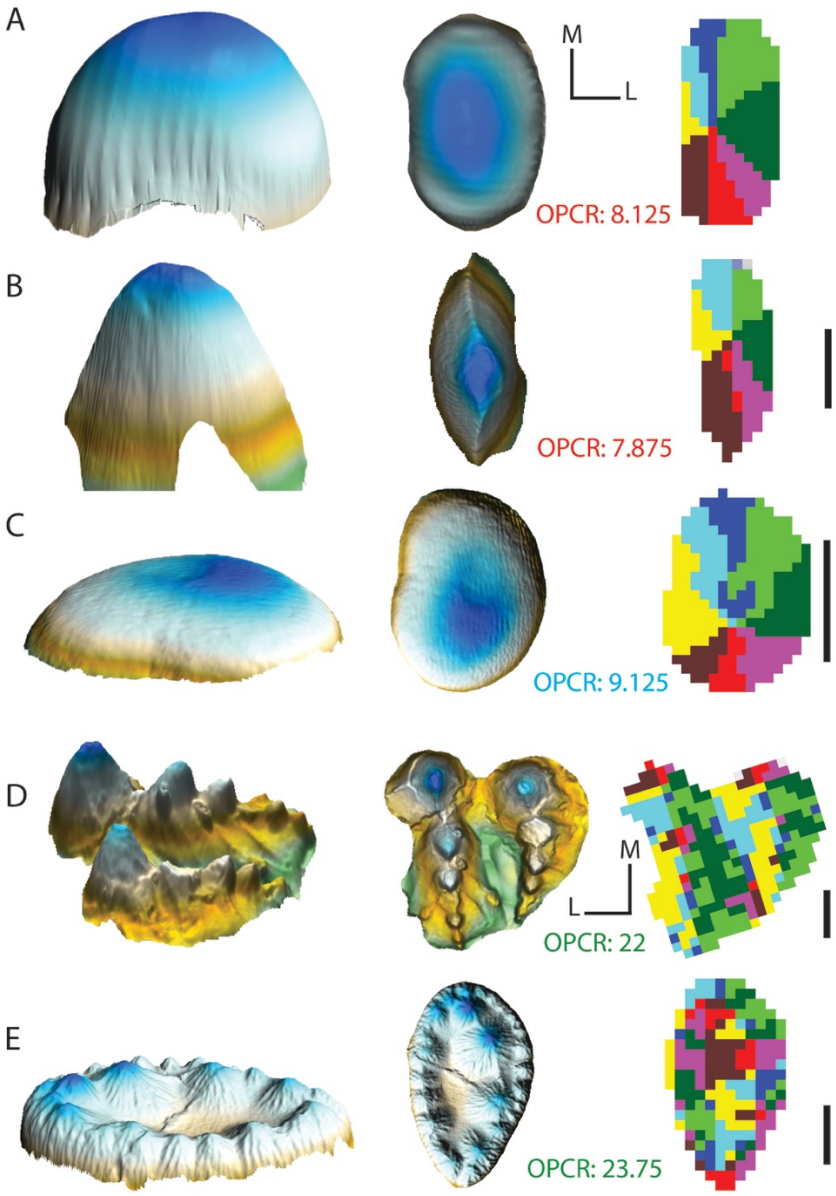


Figure 3.1- Range of dental complexity among crocodyliforms. Oblique (left) and occlusal (center) views of false color 3D models of isolated teeth in **(A)** *Caiman crocodilus* (FMNH 73711), **(B)** *Boverisuchus vorax* (UCMP 170767), **(C)** *Brachychampsa* sp. (UCMP 159000), **(D)** *Chimaerasuchus paradoxus* (IVPP V8274), and **(E)** UCMP 130082, an undescribed early crocodyliform from the Lower Jurassic Kayenta Formation. OPCR maps (right) display complexity; each color represents a different cardinal or ordinal direction. OPCR values are a numerical representation of phenotypic tooth complexity, with lower values belonging to carnivores (red font) and durophages (blue font) and higher values belonging to herbivores (green font). Abbreviations: **L**, lingual **M**, mesial; **OPCR,** orientation patch count rotated. Scale bar equals 5 mm.

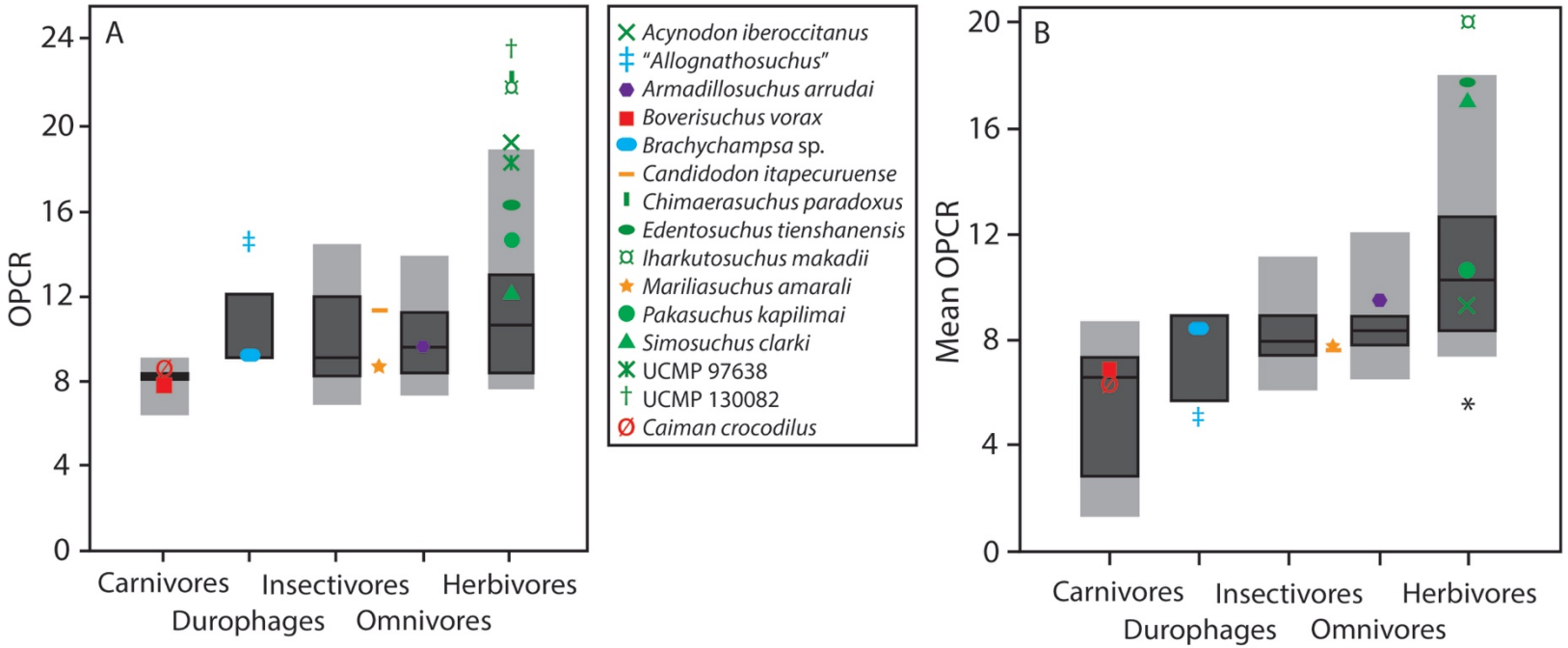


Figure 3.2- Comparison of the dental complexity of extinct crocodyliforms with extant saurians. **(A)** The most complex isolated teeth of extinct crocodyliforms compared to those of living saurians. **(B)** Diet versus mean OPCR of a tooth row (i.e., total OPCR divided by the number of teeth measured). Only crocodyliforms with four or more teeth preserved in a single tooth row were included. One extant saurian outlier, *Cyclura carinata*, is denoted with an asterisk. Dark gray boxes show median 25-75% quartiles, with the light gray boxes displaying the minimum and maximum quartiles. The median of each dietary category is designated by a horizontal line. Red symbols indicate a taxon with a carnivorous diet, blue a durophagous diet, purple an omnivorous diet, green an herbivorous diet, and orange are animals whose dental complexities could indicate either an insectivorous or omnivorous diet. Extant dataset is derived from Chapter 2.

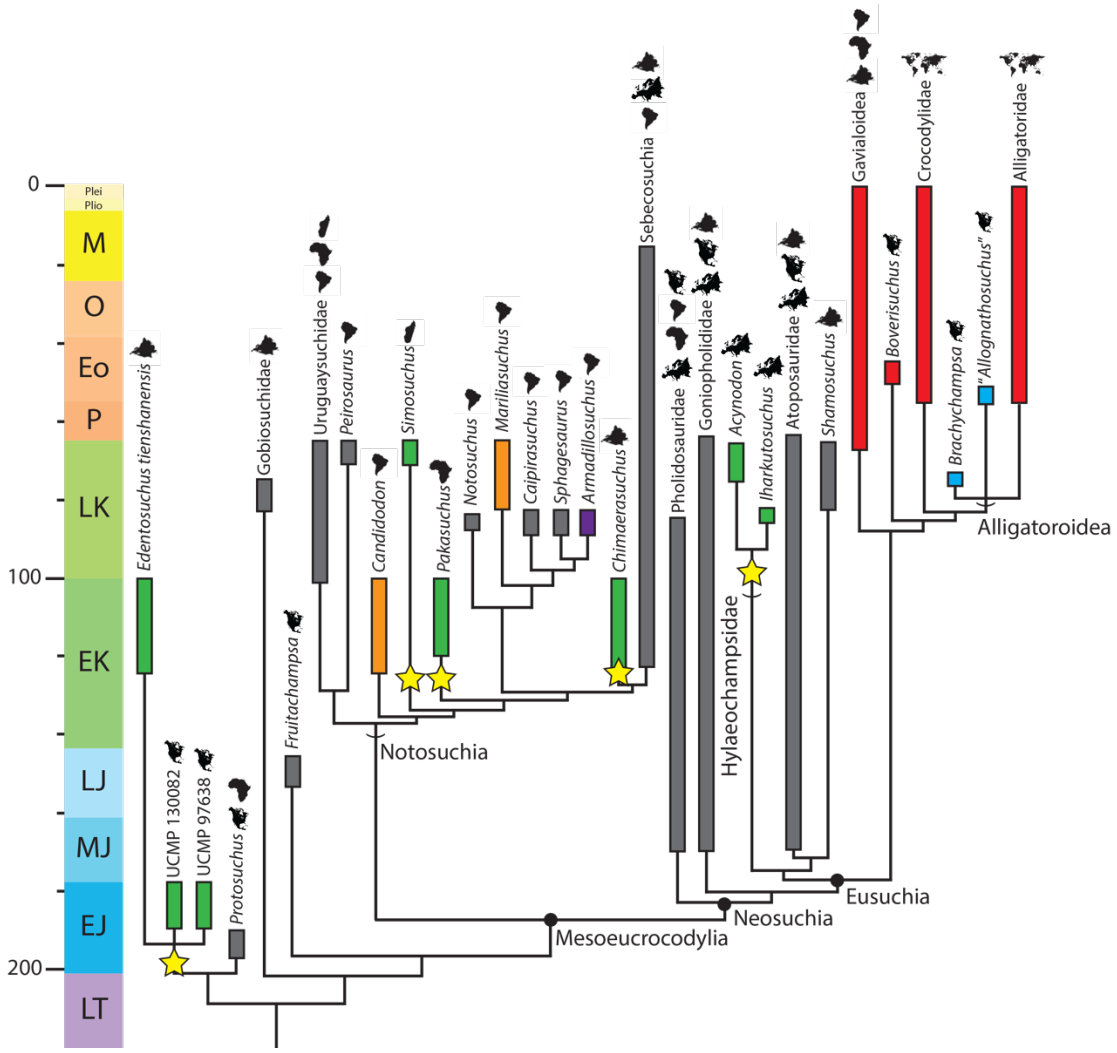


Figure 3.3- Time-calibrated phylogeny displaying reconstructed diets of extinct crocodyliforms. Stratigraphically calibrated phylogeny of crocodyliforms with location of discovery indicated by silhouettes: Africa, Asia, Australia, Europe, Madagascar, North America, and South America. Note the wide temporal and geographic extent of herbivorous crocodyliforms. Gold stars represent the evolution of herbivory. Gray boxes indicate unsampled taxa and clades, whereas the remaining box colors follow Figure 3.2. Thalattosuchia is not included because this clade was not part of the dataset and its phylogenetic position is still disputed. Phylogeny modified from Brochu (2004), Pol et al. (2004), Clark (2011), Pol et al. (2014), Turner (2015), and Young et al. (2015). Abbreviations: **EJ,** Early Jurassic; **EK,** Early Cretaceous; **Eo,** Eocene; **LJ,** Late Jurassic; **LK,** Late Cretaceous; **LT,** Late Triassic; **M,** Miocene; **MJ,** Middle Jurassic; **O,** Oligocene; **P,** Paleocene; **Plei,** Pleistocene; **Plio,** Pliocene.

Appendix

Dietary Categories

Definitions for dietary categories follow Cooper and Vitt (2002) and Chapter 2, both of which investigated diet in living saurians. Carnivores are defined as animals that primarily consume vertebrate material for greater than 90% of their diet. Although the selection of 10% plant matter in a diet is arbitrary, it allows for animals that rarely or accidentally consume plant matter to still be considered carnivores. Durophages are a special category of carnivores that preferentially consume shelled organisms, such as snails or mollusks, for a large portion of their diet. Insectivores, similar to carnivores, are defined as organisms whose diet is over 90% animal material, but has a reliance on terrestrial arthropod prey (e.g., insects), as opposed to vertebrates. The diet of omnivores varies between 10% and 90% vegetation. Herbivores are defined as animals where plants make up over 90% of the diet (Cooper and Vitt, 2002). Similar to carnivores that consume small amounts of plant material, both mammalian and reptilian herbivores are also known to occasionally, but purposely, consume animal material (Furness, 1988a; b; Greene, 1982; Iverson, 1979; Loftin and Tyson, 1965). Therefore, an herbivore may have a diet that is occasionally supplemented with vertebrate and/or invertebrate material.

Data Collection and Analysis

Extant saurian data are derived from Chapter 2. To generate the data for the OPCR analyses in this study, I utilized μCT scans of the dental rows and isolated teeth of 14 extinct crocodyliforms (i.e., premaxillae, maxillae, and dentaries). A combination of fossil jaws and casts were scanned. I scanned casts of casts for *Acynodon iberoccitanus*, *Armadillosuchus arrudai*, *Candidodon itapecuruense*, *Edentosuchus tienshanensis*,

Mariliasuchus amarali, *Chimaerasuchus paradoxus*, and *Iharkutosuchus makadii* from molds made by Ősi (2013) using Coltene President Jet Regular (polysiloxane vinyl). I also molded and cast "*Allognathosuchus*" and *Boverisuchus* specimens from the University of California Museum of Paleontology. Molds were made of Reprosil light body catalyst and base molding material and casts were produced with EPOTEK 301 epoxy resin (see Chapter 1), which has a resolution of a fraction of a micron (Teaford and Oyen, 1989). The original specimen of *Brachychampsa* sp. (UCMP 159000) was scanned rather than molded and cast.

All specimens except *Simosuchus clarki*, UCMP 97638, and UCMP 130082 were μCT scanned at the University of Utah Small Animal Imaging Core Facility. A Siemens INVEON μCT scanner digitized each jaw at a voxel resolution of 35 microns, a voltage of 80 kVp, and a current of 150 μA. Multiple specimens were scanned together at a pixel resolution of 1152; each scan comprised 1,984 or 2,016 slices. *Simosuchus* was μCT scanned at the University of Texas at Austin High Resolution X-ray Computed Tomography Facility (HRXCT) and a detailed description of the scanning protocol is available in Kley et al. (2010). UCMP 97638 and UCMP 130082 were scanned at the same HRXCT facility by C.M. Holliday (University of Missouri); these scans have a voxel resolution of 12.11 and 14.75 microns, respectively.

Scan data were processed and converted into digital elevation models following the methodology in Chapter 1. Dental complexity was quantified using the Orientation Patch Count (OPC) method. OPC quantifies dental complexity by determining the surface orientation of each pixel in the digital elevation model and grouping contiguous pixels facing the same cardinal and ordinal directions (e.g., north, south, southwest) into

'patches'. The number of patches in the tooth row is the numerical representation of dental complexity. Slight variations in tooth orientation are mitigated by repeating the OPC calculation eight times at rotations of multiples of 5.625˚. The mean of these separate tests is called Orientation Patch Count Rotated (OPCR), which is reported here.

To reduce the impact of size on shape, all teeth were scaled to the same sizes, 25, 40, and 50 pixel rows (Chapter 2). The main data presented in this chapter are the results of 25 data rows per tooth (RPT) analyses. Although they represent the lowest resolution tests, the effect of large cracks, tooth wear, other damage, and differences in scan resolution are largely removed, which is not the case in higher resolution OPC analyses.

Institutional Abbreviations

ACAP, Association Culturelle, Archéologique et Paléontologique de l'Ouest Biterrois, Cruzy, Hérault, France; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **MN,** Museu Nacional, Rio de Janeiro, Brazil; **MPMA,** Museu de Paleontologia de Monte de Alto, Monte Alto, Brasil; **MTM,** Hungarian Natural History Museum, Budapest, Hungary; **RRBP,** Rukwa Rift Basin Project, Tanzanian Antiquities Unit, Dar es Salaam, Tanzania; **UA,** University of Antananarivo, Antananarivo, Madagascar; **UCMP,** Museum of Paleontology, University of California, Berkeley, CA, USA; **UFRJ,** Universidad Federal do Rio de Janeiro, Brazil.

Table S.3.1- The total number of patches per isolated tooth (OPCRit) of fossil crocodyliforms at 25, 40, and 50 data rows per tooth (RPT). Each tooth measured was the most complex tooth in the jaw.

Taxon	Specimen number	Element Measured	Tooth Measured	OPCR: 50 RPT	OPCR: 40 RPT	OPCR: 25 RPT	Type	UMNH VP C-#
Acynodon iberoccitanus	ACAP-FX2	Left Maxilla	16	49.25	36.5	19	Cast	326
"*Allognathosuchus*"	UCMP 150180	Left Dentary	4	37.875	25.375	14.75	Cast	330
Armadillosuchus arrudai	MPMA-64-0001-04	Right Maxilla	1	16.625	13.5	9.75	Cast	332
Boverisuchus vorax	UCMP 170767	Right Dentary	5	13.25	11	7.875	Cast	335
Brachychampsa sp.	UCMP 159000	Left Dentary	16	13.375	10.625	9.125	Bone	-
Candidodon itapecuruense	UFRJ DG 114-R	Right Maxilla	9?	46.875	30.875	11.375	Cast	337
Chimaerasuchus paradoxus	IVPP V8274	Left Maxilla	4	69.375	51	22	Cast	339
Edentosuchus tienshanensis	IVPP V3236	Right Dentary	6	31.375	26.75	16.25	Cast	340
Iharkutosuchus makadii	MTM 2006.52.1	Left Maxilla	17	72.75	47.25	21.75	Cast	341
Mariliasuchus amarali	MN 6756-V	Right Dentary	7	17.75	13.375	8.75	Cast	345
Pakasuchus kapilimai	RRBP 08631	Left Maxilla	3	22.875	21	14.75	Bone	-
Simosuchus clarki	UA 8679	Left Dentary	1	18.375	17	12.25	Bone	-
UCMP 97638	UCMP 97638	Left Dentary	5	58.625	37.75	18.25	Bone	-
UCMP 130082	UCMP 130082	Left Dentary	?	78.625	51.375	23.75	Bone	-

Table S.3.2- The total and average patches per tooth (OPCRavg) in fossil crocodyliforms with greater than four teeth preserved at 25, 40, and 50 data rows per tooth (RPT).

Taxon	Specimen number	Element Measured	# of Teeth Measured	Total OPCR	OPCRavg	Type	UMNH VP C-#
Acynodon iberoccitanus	ACAP-FX2	Right Maxilla	6	55.375	9.229	Cast	326
"*Allognathosuchus*"	UCMP 150180	Left Dentary	5	24.875	4.975	Cast	330
Armadillosuchus arrudai	MPMA-64-0001-04	Right Maxilla and Premaxilla	4	37.75	9.438	Cast	332
Boverisuchus vorax	UCMP 170767	Right Dentary	6	42.25	7.042	Cast	335
Brachychampsa sp.	UCMP 159000	Left Dentary	12	101	8.417	Bone	-
Candidodon itapecuruense	UFRJ DG 114-R	Left Maxilla	6	46.625	7.771	Cast	337
Edentosuchus tienshanensis	IVPP V3236	Right Dentary	7	124	17.714	Cast	340
Iharkutosuchus makadii	MTM 2006.52.1	Left Maxilla	5	99.875	19.975	Cast	341
Mariliasuchus amarali	MN 6298-V, MN 6756-V	Left Dentary	6	46.625	7.771	Cast	345, 346
Pakasuchus kapilimai	RRBP 08631	Left Maxilla	4	43.125	10.781	Bone	-
Simosuchus clarki	UA 8679	Left Dentary	5	85	17	Bone	-

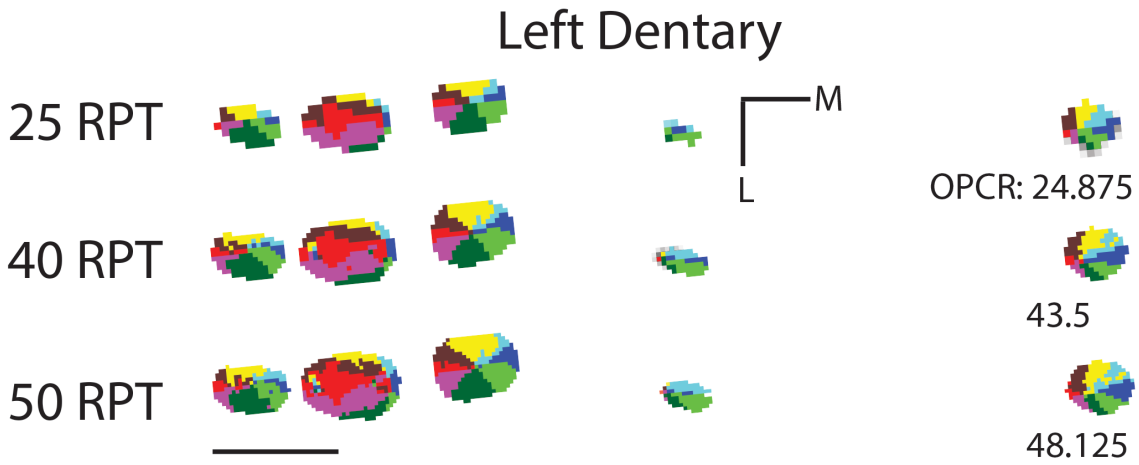


Figure S.3.1- OPCR maps of "*Allognathosuchus*" (UCMP 150180) left dentary. Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

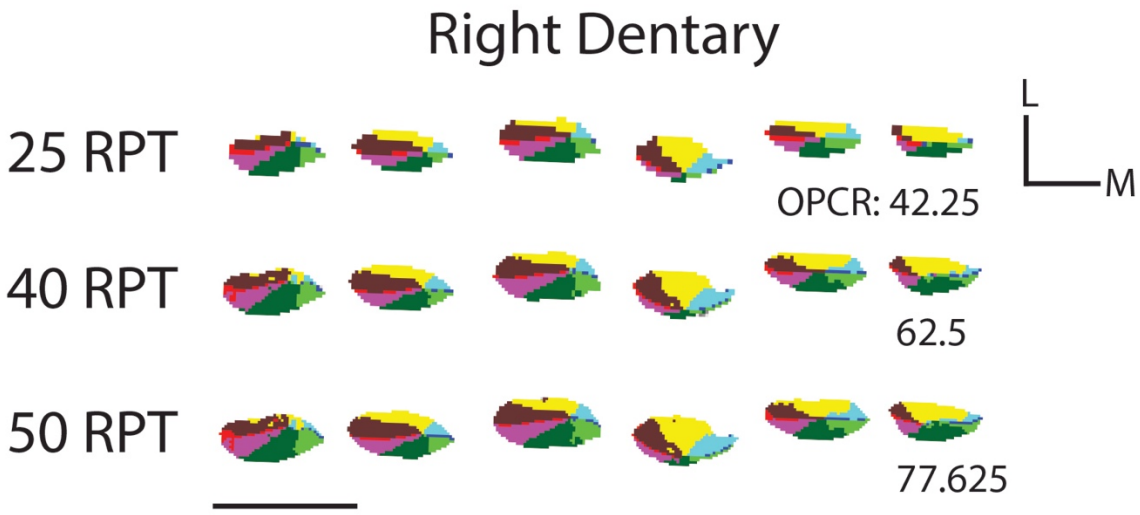


Figure S.3.2- OPCR maps of *Boverisuchus vorax* (UCMP 170767). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

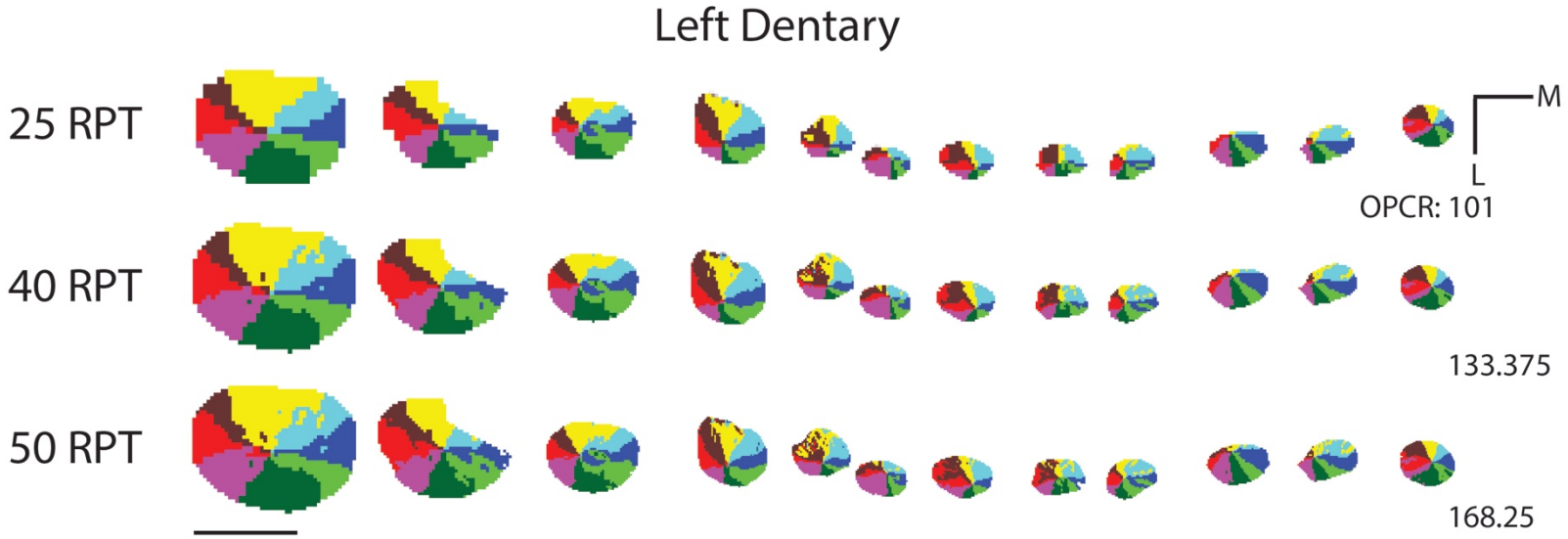


Figure S.3.3- OPCR maps of *Brachychampsa sp.* (UCMP 159000). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

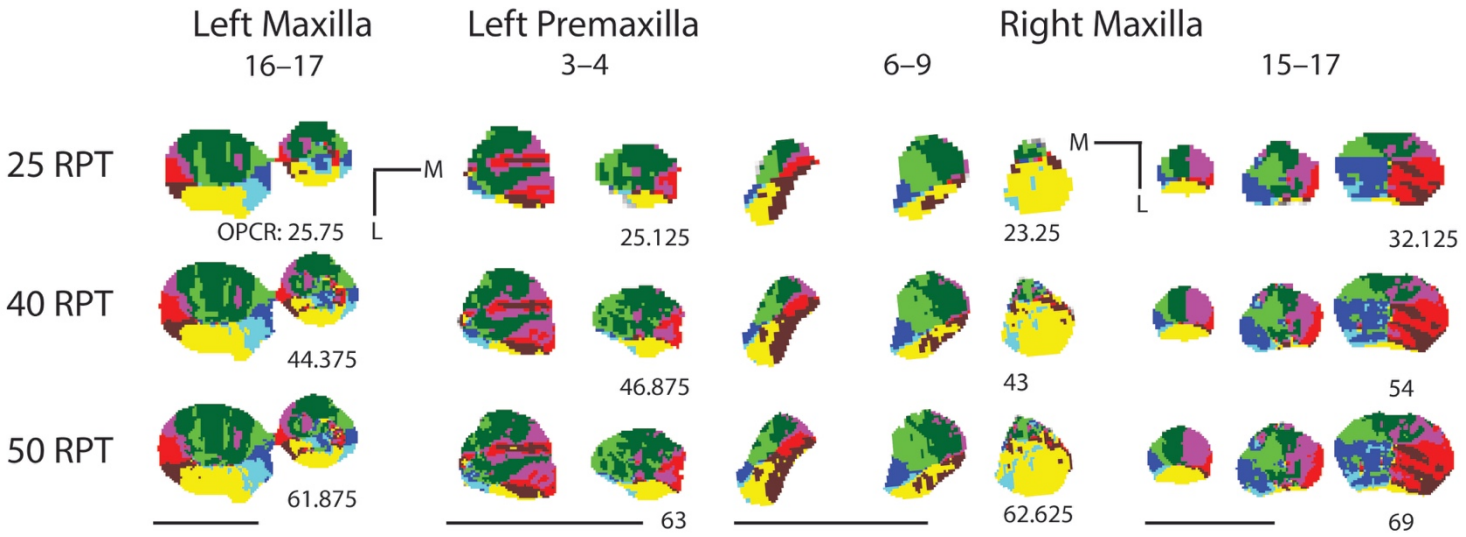


Figure S.3.4- OPCR maps of *Acynodon iberoccitanus* (ACAP-FX2). Number below element indicate tooth position in each respective element. Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bars equal 1.0 cm.

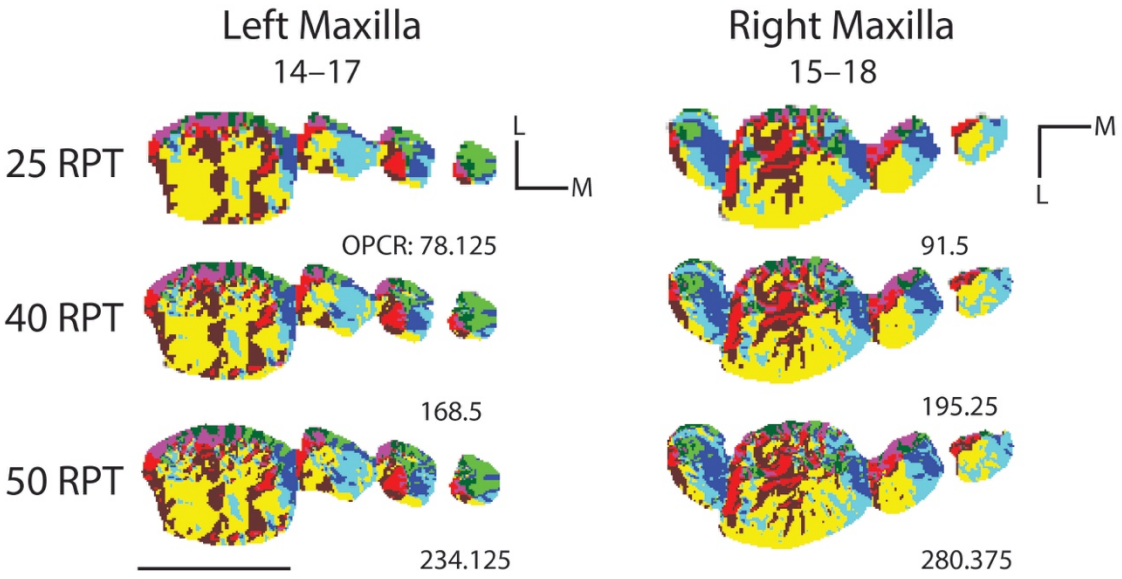


Figure S.3.5- OPCR maps of *Iharkutosuchus makadii* (MTM 2006.52.1). Number below element indicate tooth position in each respective element. Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

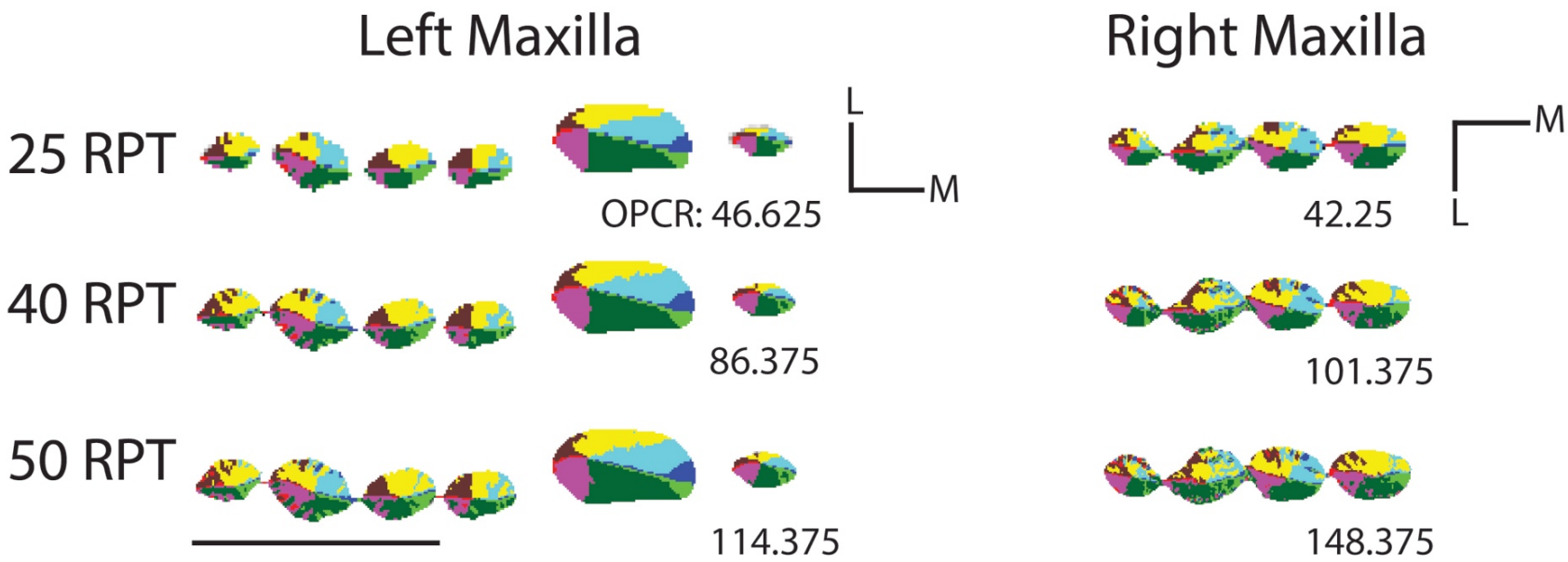


Figure S.3.6- OPCR maps of *Candidodon itapecuruense* (UFRJ DG 114-R). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

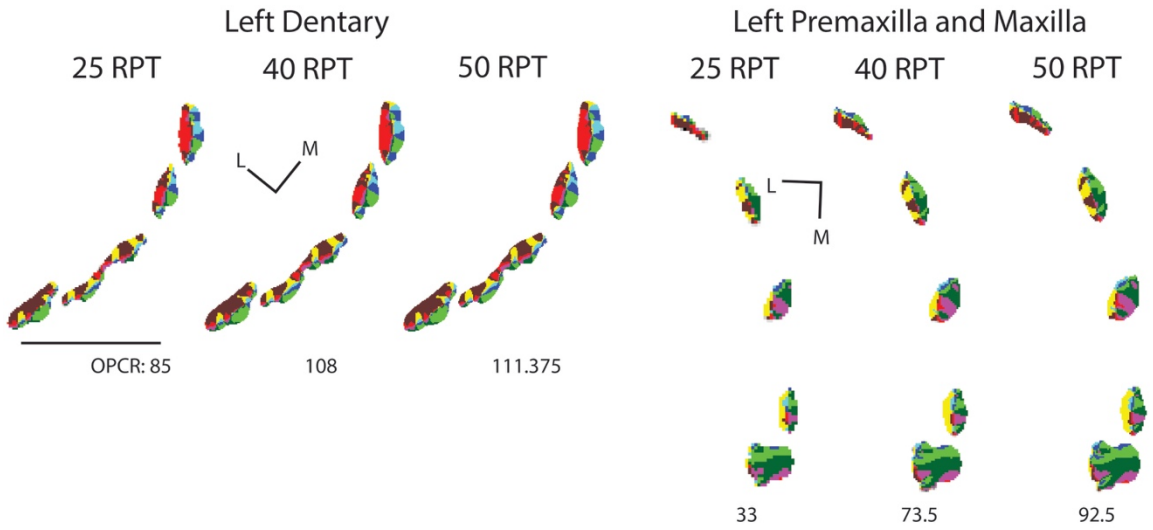


Figure S.3.7- OPCR maps of *Simosuchus clarki* (IVPP V3236). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

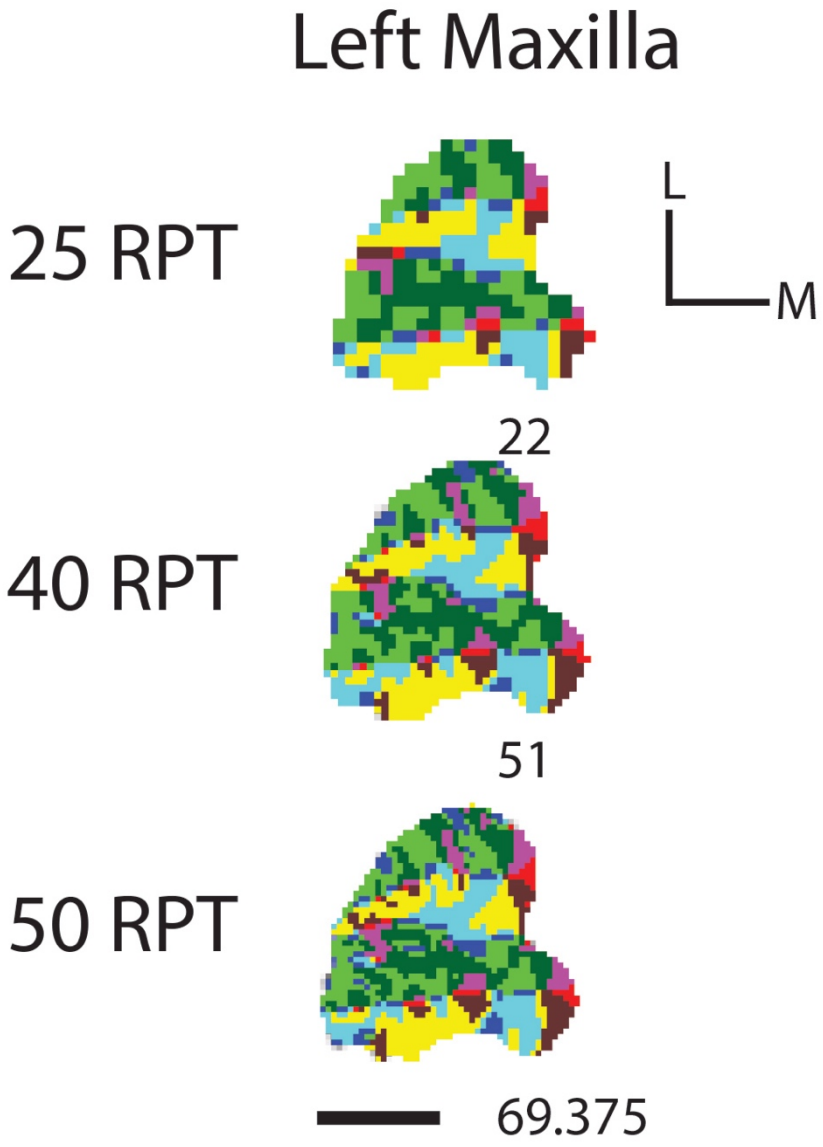


Figure S.3.8- OPCR maps of *Chimaerasuchus paradoxus* (IVPP V8274). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

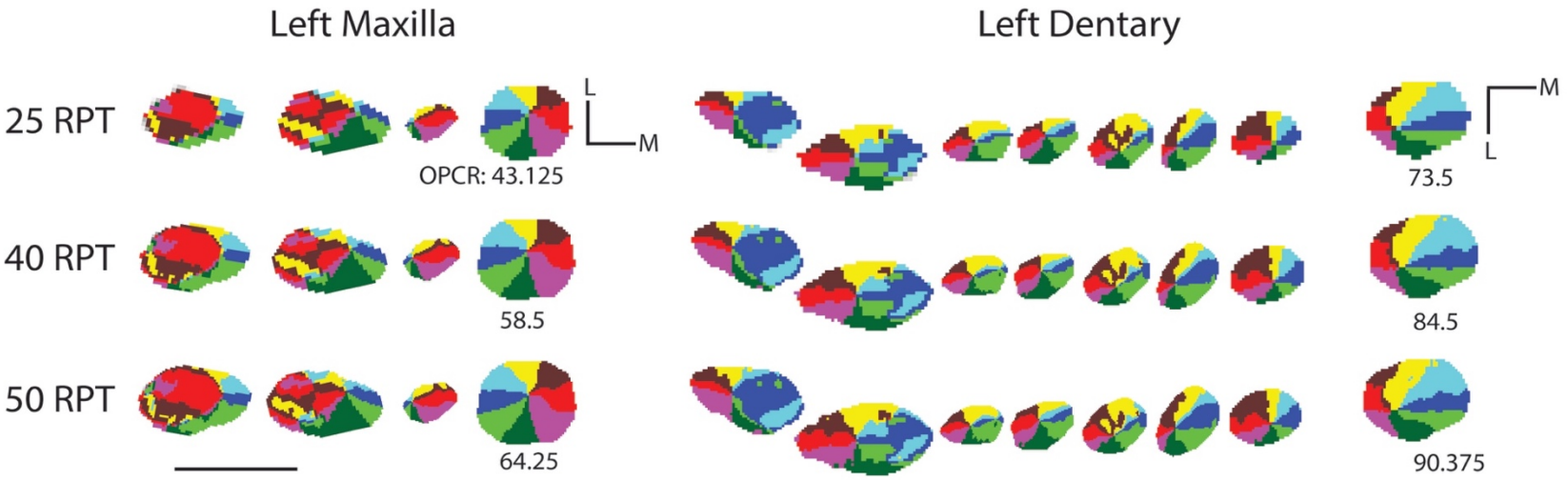


Figure S.3.9- OPCR maps of *Pakasuchus kapilimai* (RRBP 08631). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

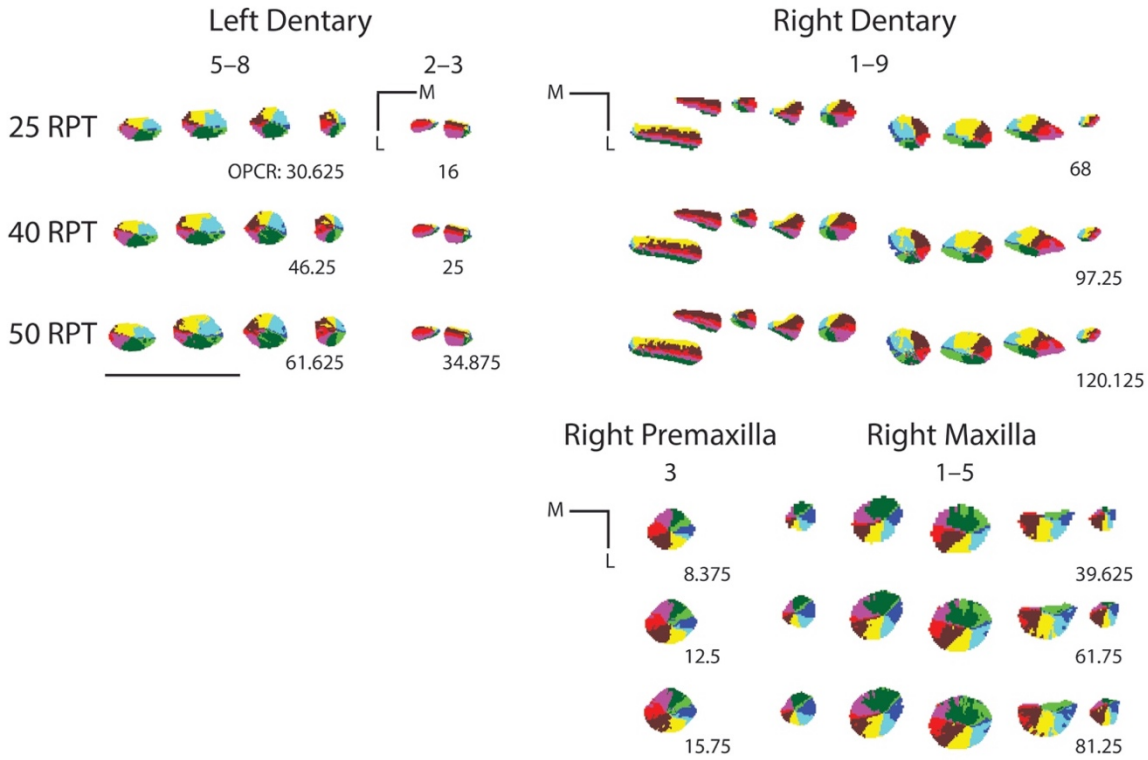


Figure S.3.10- OPCR maps of *Mariliasuchus amarali* (MN 6756-V). Number below element indicate tooth position in each respective element. Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

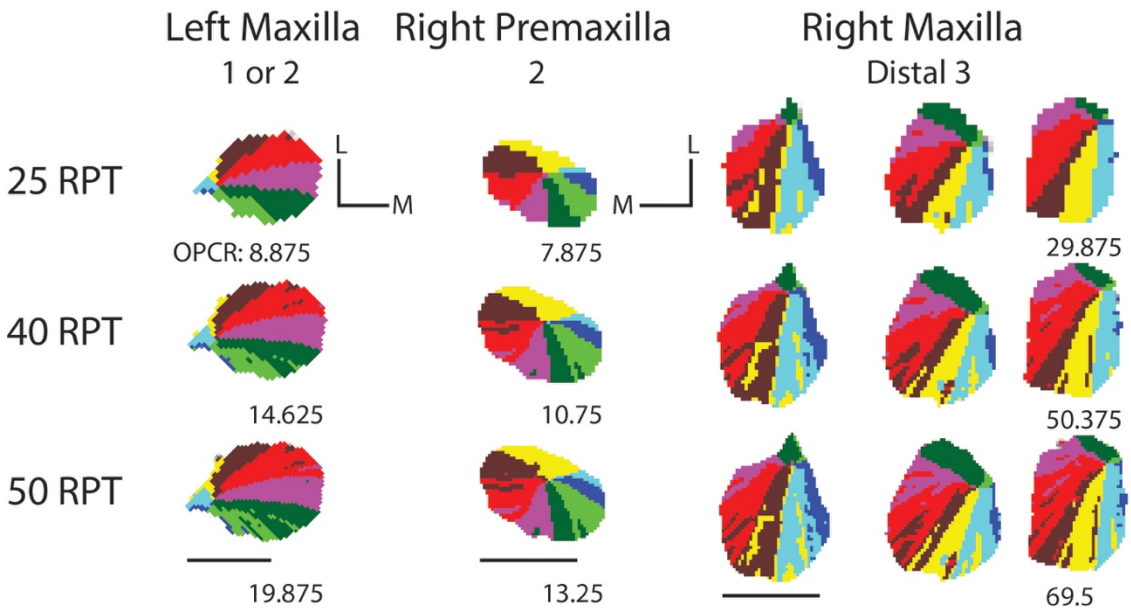


Figure S.3.11- OPCR maps of *Armadillosuchus arrudai* (MPMA-64-0001-04). Number below element indicate tooth position in each respective element. Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bars equal 1.0 cm.

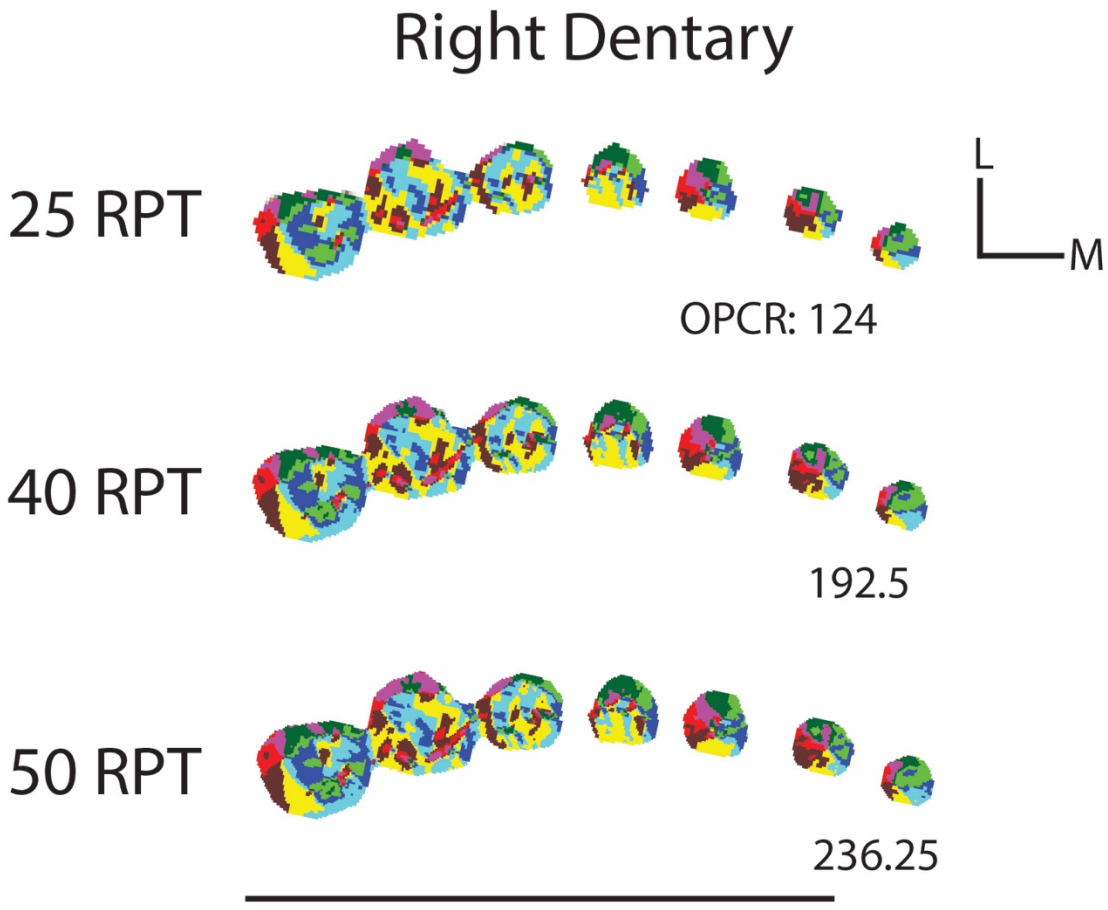


Figure S.3.12- OPCR maps of *Edentosuchus tienshanensis* (IVPP V3236). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

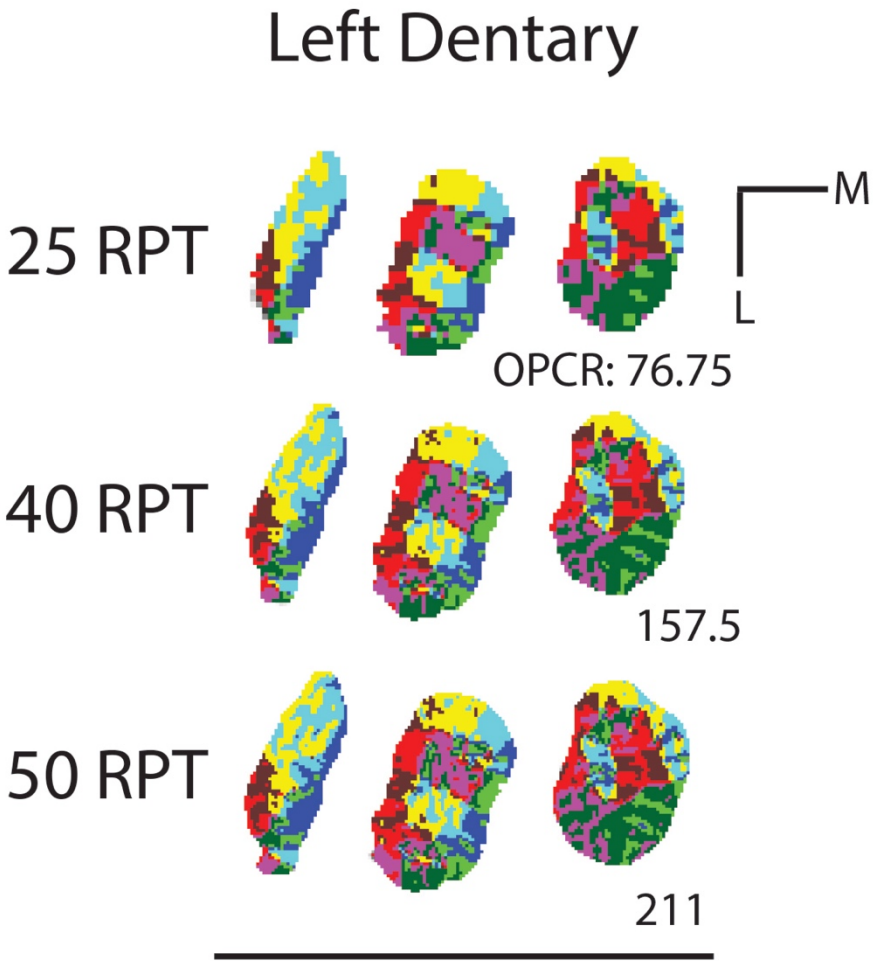


Figure S.3.13- OPCR maps of an unnamed early crocodyliform from the Lower Jurassic Kayenta Formation (UCMP 97638). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

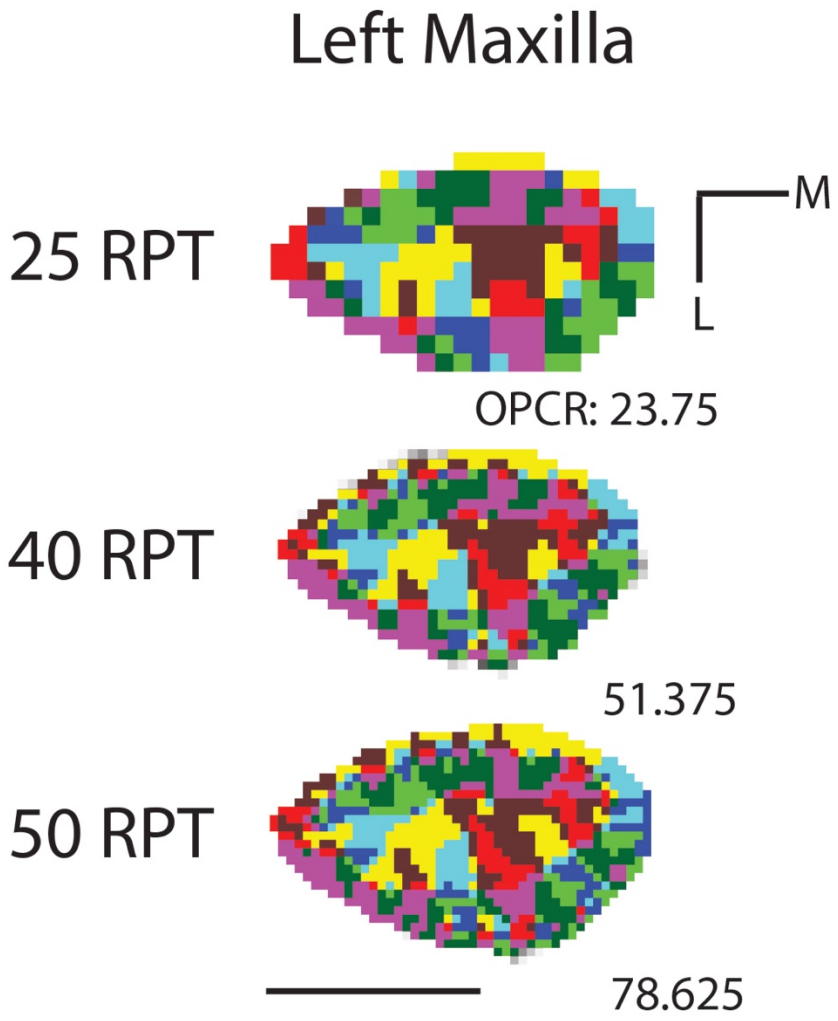


Figure S.3.14- OPCR maps of an unnamed early crocodyliform from the Lower Jurassic Kayenta Formation (UCMP 130082). Abbreviations: **L**, lingual **M**, mesial; **OPCR**, orientation patch count rotated; **RPT,** rows per tooth. Scale bar equals 1.0 cm.

References

Barrett, P. M. 2000. Prosauropod dinosaurs and iguanas - speculations on the diets of extinct reptiles; pp. 42–78 in H. D. Sues (ed.), Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record.

Benton, M. J., and J. M. Clark. 1988. Archosaur phylogeny and the relationships of the Crocodylia; pp. 95–338 in M. J. Benton (ed.), The Phylogeny and Classification of the Tetrapods. Clarendon Press, London.

Brochu, C. A. 2004. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. Journal of Vertebrate Paleontology 24:857–873.

Buckley, G. A., C. A. Brochu, D. W. Krause, and D. Pol. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. Nature 405:941–944.

Clark, J. M. 1994. Patterns of evolution in Mesozoic Crocodyliformes; pp. 84–97 in N. Fraser, and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge.

Clark, J. M. 2011. A new shartegosuchid crocodyliform from the Upper Jurassic Morrison Formation of western Colorado. Zoological Journal of the Linnean Society 163:S152–S172.

Clark, J. M., L. L. Jacobs, and W. R. Downs. 1989. Mammal-like dentition in a Mesozoic crocodylian. Science 244:1064–1066.

Csiki-Sava, Z., E. Buffetaut, A. Ősi, X. Pereda-Suberbiola, and S. L. Brusatte. 2015. Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land- living vertebrates on the Late Cretaceous European archipelago. ZooKeys 469:1–161.

D'Amore, D. C., and R. J. Blumenschine. 2009. Komodo monitor (*Varanus komodoensis*) feeding behavior and dental function reflected through tooth marks on bone surfaces, and the application to ziphodont paleobiology. Paleobiology 35:525–552.

Evans, A. R., and C. M. Janis. 2014. The evolution of high dental complexity in the horse lineage. Annales Zoologici Fennici 51:73–79.

Evans, A. R., G. P. Wilson, M. Fortelius, and J. Jernvall. 2007. High-level similarity of dentitions in carnivorans and rodents. Nature 445:78–81.

Furness, R. W. 1988a. The predation of Tern chicks by sheep. Bird Study 35:199–202.

Furness, R. W. 1988b. Predation on ground-nesting seabirds by island populations of red

deer *Cervus elaphus* and sheep *Orvis*. Journal of Zoology 216:565–573.

Fiorelli, L., and J. O. Calvo. 2008. New remains of *Notosuchus terrestris* Woodward, 1896 (Crocodyliformes: Mesoeucrocodylia) from Late Cretaceous of Neuquen, Patagonia, Argentina. Arquivos do Museu Nacional, Rio de Janeiro 66:83–124.

Gomani, E. M. 1997. A crocodyliform from the Early Cretaceous of Malawi. Journal of Vertebrate Paleontology 17:280–294.

Greene, H. W. 1982. Dietary and phenotypic diversity in lizards: why are some organisms specialized?; pp 107–128 in D. Mossakowski and G. Roth (eds), Environmental Adaptation and Evolution.: Gustav Fischer, New York, New York.

Head, J. J., G. F. Gunnel, P. A. Holroyd, J. H. Hutchinson, and R. L. Ciochon. 2013. Giant lizards occupied herbivorous mammalian ecospace during the Paleogene greenhouse in Southeast Asia. Proceedings on the Royal Society B 280:20130665

Hotton, N. 1955. A Survey of Adaptive Relationships of Dentition to Diet in the North American Iguanidae. American Midland Naturalist 53:88–114.

Iverson, J. B. 1979. Behavior and ecology of the rock iguana *Cyclura carinata*. Bulletin of the Florida State Museum: Biological Sciences 24:175–358.

Jenkins, F. A., A. W. Crompton, and W. R. Downs. 1983. Mesozoic Mammals from Arizona: New Evidence on Mammalian Evolution. Science 222:1233–1235.

Kley, N. J., J. J. W. Sertich, A. H. Turner, D. W. Krause, P. M. O'Connor, and J. A. Georgi. 2010. Craniofacial morphology of *Simosuchus clarki* (Crocodyliformes: Notosuchia) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 30:13–98.

Krause, D. W., M. D. Gottfried, P. M. O'Connor, and E. M. Roberts. 2003. A Cretaceous mammal from Tanzania. Acta Palaeontologica Polonica 48:321–330.

Kühne, W. G. 1956. The Liassic Therapsid *Oligokyphus*. 149 pp. British Museum (Natural History), London.

Larson, D. W., and D. C. Evans. 2015. Ecomorphological relationships between diet and morphology in extant *Varanus* lizards. Journal of Vertebrate Paleontology 35:160A.

Loftin, H., and E. L. Tyson. 1965. Iguanas as carrion eaters. Copeia 1965:515.

Lopatin, A., and A. Averianov. 2015. *Gobiconodon* (Mammalia) from the Early Cretaceous of Mongolia and Revision of Gobiconodontidae. Journal of Mammal Evolution 22:17–43.

Luo, Z. X., P. Chen, G. Li, and M. Chen. 2007. A new eutriconodont mammal and evolutionary development in early mammals. Nature 446:288–293.

Marinho, T. S., and I. S. Carvalho. 2009. An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. Journal of South American Earth Sciences 27:36–41.

O'Connor, P. M., J. J. Sertich, N. J. Stevens, E. M. Roberts, M. D. Gottfried, T. L. Hieronymus, Z. A. Jinnah, R. Ridgely, S. E. Ngasala, and J. Temba. 2010. The evolution of mammal-like crocodyliforms in the Cretaceous Period of Gondwana. Nature 466:748–751.

Ősi, A. 2013. The evolution of jaw mechanism and dental function in heterodont crocodyliforms. Historical Biology 26:279–414.

Ősi, A., and D. B. Weishampel. 2009. Jaw mechanism and dental function in the Late Cretaceous basal eusuchian *Iharkutosuchus*. J Morphol 270:903–920.

Pol, D., S. Ji, J. M. Clark, and L. M. Chiappe. 2004. Basal crocodyliforms from the Lower Cretaceous Tugulu Group (Xinjiang, China), and the phylogenetic position of *Edentosuchus*. Cretaceous Research 25:603–622.

Pol, D., P. M. Nascimento, A. B. Carvalho, C. Riccomini, R. A. Pires-Domingues, and H. Zaher. 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. PLOS ONE 9:e93105.

Rogers, R. R., D. W. Krause, S. C. Kast, M. S. Marshall, L. Rahantarisoa, C. R. Robins, and J. J. W. Sertich. 2013. A new, richly fossiliferous member comprised of tidal deposits in the Upper Cretaceous Maevarano Formation, northwestern Madagascar. Cretaceous Research 44:12–29.

Santana, S. E., S. Strait, and E. R. Dumont. 2011. The better to eat you with: functional correlates of tooth structure in bats. Functional Ecology 25:839–847.

Schultz, J. A., D. W. Krause, W. von Koenigswald, and E. R. Dumont. 2014. Dental Function and Diet of *Vintana sertichi* (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar. Journal of Vertebrate Paleontology 34:182–202.

Sereno, P., and H. Larsson. 2009. Cretaceous Crocodyliforms from the Sahara. ZooKeys 28:1–143.

Smith, T., and V. Codrea. 2015. Red iron-pigmented tooth enamel in a multituberculate mammal from the Late Cretaceous Transylvanian “Haţeg Island”. PLoSONE 10:e0132550.

Smits, P. D., and A. R. Evans. 2012. Functional constraints on tooth morphology in

carnivorous mammals. BMC Evolutionary Biology 12:146.

Soto, M., D. Pol, and D. Perea. 2011. A new specimen of *Uruguaysuchus aznarezi* (Crocodyliformes: Notosuchia) from the middle Cretaceous of Uruguay and its phylogenetic relationships. Zoological Journal of the Linnean Society 163:173–198.

Stubbs, T. L., S. E. Pierce, E. J. Rayfield, and P. S. Anderson. 2013. Morphological and biomechanical disparity of crocodile-line archosaurs following the end-Triassic extinction. Proceedings of the Royal Society B 280:20131940.

Sues, H. D. 1986. The Skull and Dentition of Two Tritylodontid Synapsids from the Lower Jurassic of Western North America. Bulletin of the Museum of Comparative Zoology at Harvard College 151:217–268.

Sues, H. D., J. M. Clark, and F. A. Jenkins. 1994. A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest; pp. 284–294 in N. Fraser, and H. D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge, UK.

Teaford, M. F., and O. J. Oyen. 1989. Live Primates and Dental Replication: New Problems and New Techniques. American Journal of Physical Anthroplogy 83:73–81.

Turner, A. H. 2015. A Review of *Shamosuchus* and *Paralligator* (Crocodyliformes, Neosuchia) from the Cretaceous of Asia. PLOS ONE 10:e0118116.

Tykoski, R. S. 2005. Vertebrate paleontology in the Arizona Jurassic; pp. 72–93 in R. D. McCord (ed.), Mesa Southwest Museum Bulletin. Southwest Paleontological Society, Mesa, Az.

Wilson, G. P., A. R. Evans, I. J. Corfe, P. D. Smits, M. Fortelius, and J. Jernvall. 2012. Adaptive radiation of multituberculate mammals before the extinction of dinosaurs. Nature 483:457–460.

Winchester, J. M., D. M. Boyer, E. M. St. Clair, A. D. Gosselin-Ildari, S. B. Cooke, and J. A. Ledogar. 2014. Dental Topography of Platyrrhines and Prosimians: Convergence and Contrasts. American Journal of Physical Anthropology 153:29–44.

Wu, X.-C., and H.-D. Sues. 1996. Anatomy and Phylogenetic Relationships of *Chimaerasuchus paradoxus*, an Unusual Crocodyliform Reptile from the Lower Cretaceous of Hubei, China. Journal of Vertebrate Paleontology 16:688–702.

Wu, X.-C., H.-D. Sues, and A. Sun. 1995. A plant-eating crocodyliform from the Cretaceous of China. Nature 376:678–680.

Young, M. T., S. L. Brusatte, M. Ruta, and M. B. De Andrade. 2010. The evolution of Metriorhynchoidea (mesoeucrocodylia, thalattosuchia): an integrated approach using geometric morphometrics, analysis of disparity, and biomechanics. Zoological Journal of the Linnean Society 158:801–859.

Zhou, Z., P. M. Barrett, and J. Hilton. 2003. An exceptionally preserved Lower Cretaceous ecosystem. Nature 421:807–814.